ALCOHOLISM AND THE GROWTH OF WHITE RATS

E. CARLETON MACDOWELL[1]

Station for Experimental Evolution, Cold Spring Harbor, Long Island, New York

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INTRODUCTION

The data for this paper were collected in connection with experiments undertaken with the primary purpose of studying possible methods of modifying and controlling heritable characters, especially of a psychological nature. Attention is here directed to the immediate effect of alcohol fumes upon the weight of the treated animals, as well as upon the weight of their descendants. It is fully recognized that weight is an exceedingly complicated character, the result of the interaction of a great number of influences in which environmental factors and nutrition play a large part. However, under the experimental conditions of the laboratory, these last influences are largely equalized for all the animals and even if it is impossible to make definite interpretations of the channels by which the final effects upon weight are brought about, the conclusions in themselves may be of some value. PEARL (1917, p. 171) made this statement: "Clinical experience has abundantly demonstrated that body-weight

[1] Many of the data upon which this paper is based were recorded by Miss E. M. VICARI who has taken an active part in carrying out the experiments and in whose charge the whole work was left during the author's absence in 1917 and 1918. The charts were constructed by Mr. LAURENCE H. SNYDER, who has carried through a large part of the statistical work involved.

changes, in spite of their rough and inexact character, furnish an index of general metabolic conditions and changes, which is by no means to be despised." The results here presented indicate that, instead of causing any direct demonstrable genetic change, the treatment has had a definite physiological effect upon the treated animals and, perhaps through this, has acted as a selective agent upon genetic differences that were already present.

METHODS

Full details of the relationships of the rats used, the methods of breeding and the treatment, have already been published (MACDOWELL 1921) so it will not be necessary to repeat these details at this time. However, a full understanding of the nature of the controls employed is vital to the proper evaluation of the results here recorded. The females in a litter were divided into two groups at random: those to be treated and those to be used as controls; in like manner the males in a litter were divided into two similar groups. The matings were all between full brothers and sisters from the same single pair of grandparents as well as from the same parents; treated rats were mated in all cases with treated rats and controls with controls. In the following generations the controls were always the offspring of the controls in the preceding generations, and they were raised at the same time and under the same environmental conditions as the descendants of the treated rats in the corresponding generation. As far as is known, no other experiment of this nature has been reported with controls so strictly comparable. PEARL (1917) fully recognized the importance of using controls comparable genetically, as well as otherwise, and planned to use brothers and sisters of his treated fowl as controls, but these plans failed to materialize. STOCKARD and PAPANICOLAOU (1918) used guinea-pigs from the same stocks and blood lines and even used the same animals before treatment as a basis of estimating the effects of the alcohol treatment, but in this case the age factor is not equal in the two sets, and no comparable data on growth could be obtained. NICE (1912) and ARLITT (1919) merely used animals from the same dealers, as controls. NICE (1913) used mice in the fourth inbred generation from a single pair; NICE (1917) took all his mice from one strain which had been inbred for four generations after its start as the result of crossing two entirely distinct strains.

The alcohol was administered by the inhalation method. The treatment for both males and females started at the age of twenty-eight days, when they were weaned; to the males it was given daily throughout life;

to the females it was given daily with the exception of the twenty-eight days of nursing after the birth of each litter. The amount of alcohol inhaled was measured by the reactions of the rats. After the first days, when the treatment was lighter, they were left in the tanks until they were fully anesthetized, that is, limp and motionless.

The rats were raised on a diet of bread and fresh milk every day and dog bread especially prepared for rodents was kept in the cages at all times except during the behavior tests. Since all of these rats were used in behavior tests which involved reduction in the ration, the curves are lower at certain ages than they would normally have been. In all but a few cases the rats were weighed once a week on the same day of the week, starting with the first weighing day after they were weaned and continuing through the life of the animal. In a few cases at the end of the experiment, when war conditions made it impossible to make the weighings more often, they were made once a month. All available records have been used. From these records the growth curves were plotted on large sheets at the scale of twenty grams and ten days to the inch. Being weighed on the same day of each week the rats were at different ages; this necessitated a correction in order to summarize the data. The method employed was to interpolate the values at the desired ages by reading the weight value of the intersection of the age line with the straight line connecting the actual weighings plotted on either side. The possible effect of a personal element was eliminated in this way. In a preliminary study of these data an attempt was made to estimate corrections for minor irregularities in these curves and to take into consideration all special circumstances that might appear to influence the weights as recorded. This method of estimating the readings from the growth curves is obviously too open to criticism to be employed finally, but it may be noted that the results indicated by this method of reading the curves fully agreed with those here presented.

The main conclusions must be based on the males, since most of the females were bred and their pregnancies made a serious difficulty in reading the growth curves after maturity. No formulae could be used to correct for these pregnancy peaks, since the weighings were not made in any definite relation to the birth of the litters, so that the only way to include pregnant females without including the developing foetuses seemed to be to make an estimation of the probable normal weight based on the rest of the curve in comparison with the curves of the rest of the females in the same litter. Since there were frequently pregnancies in the other females in the litter, this estimation of normal weights for the females is far from reliable. Another complication lies in the fact that the treated

TABLE 1

Averages of the weight per male rat in grams for the different strains separately and together in each of the four generations.

A. Treated males

STRAIN		40 DAYS		60 DAYS		90 DAYS		120 DAYS		150 DAYS		180 DAYS	
		Means	No.	Means	No.	Means	No.	Means	No.	Means	No.	Means	No.
A	Tests	71.24	33	115.24	33	153.35	28	193.04	23	215.00	21	235.55	18
	Controls	73.29	27	130.00	27	179.08	24	231.28	21	256.60	20	287.93	15
B	Tests	75.28	7	126.37	8	149.62	8	197.33	6	277.75	4	232.00	2
	Controls	72.00	10	133.54	11	179.55	9	248.66	6	257.00	4	256.50	2
C	Tests	67.95	20	113.80	20	142.56	16	192.06	15	213.45	11	231.77	9
	Controls	71.57	19	124.73	19	172.78	14	226.46	13	250.25	12	264.40	10
L	Tests	69.30	10	119.30	10	150.66	9	183.33	6	206.00	2	246.00	5
	Controls	76.25	8	132.37	8	172.75	8	212.33	6	239.33	3	260.60	5
All	Tests	70.43	70	116.66	71	149.63	61	192.10	50	215.39	38	235.88	34
	Controls	72.95	64	129.35	65	176.63	55	229.71	46	257.97	39	274.34	32

B. Untreated males from treated parents

A	Tests	88.75	4	100.75	4	160.50	4	246.00	4	290.50	4	314.00	4
	Controls	59.10	10	75.00	10	111.80	10	200.25	8	247.50	8	276.00	8
B	Tests	75.50	6	93.66	6	117.16	6	181.83	6	212.16	6	218.33	6
	Controls	65.60	5	88.40	5	115.00	5	173.20	5	200.20	5	203.60	5
C	Tests	86.00	4	99.50	4	137.20	4	210.25	4	253.00	4	274.00	4
	Controls	63.66	3	78.00	3	123.33	3	180.66	3	199.00	3	212.33	3
L	Tests	62.25	12	93.41	12	117.91	12	180.08	12	212.00	12	233.00	11
	Controls	67.36	11	92.18	11	123.00	11	173.45	11	214.45	11	235.09	11
All	Tests	73.03	26	95.53	26	127.26	26	195.26	26	230.42	26	249.00	25
	Controls	63.82	29	84.13	29	117.79	29	182.14	27	219.88	27	238.85	27

C. Untreated males from untreated parents and treated grandparents

A	Tests	91.25	4	122.75	4	156.50	4	235.25	4	263.25	4	240.25	4
	Controls	95.66	3	126.66	3	197.66	3	270.00	3	307.66	3	315.33	3
C	Tests	66.00	3	95.66	3	128.66	3	193.66	3	227.66	3	226.33	3
	Controls	72.00	3	75.66	3	83.33	3	153.00	3	183.66	3	189.33	3
L	Tests	65.33	3	111.25	4	108.75	4	146.50	4	187.75	4	237.75	4
	Controls	61.00	1	91.25	4	104.00	4	111.00	4	151.50	4	197.00	4
All	Tests	75.90	10	111.18	11	131.54	11	191.63	11	226.09	11	235.54	11
	Controls	80.57	7	97.20	10	125.90	10	171.30	10	208.00	10	230.20	10

TABLE 1 (continued)

D. Treated males from treated parents

STRAIN		40 DAYS		60 DAYS		90 DAYS		120 DAYS		150 DAYS		180 DAYS	
		Means	No.	Means	No.	Means	No.	Means	No.	Means	No.	Means	No.
C	Tests	84.33	9	132.55	9	163.75	8	203.50	8	237.36	6	278.75	4
	Controls	81.10	10	136.00	10	161.60	10	202.88	9	234.88	9	255.37	8
L	Tests	83.16	6	121.16	6	170.16	6	190.83	6	219.33	6	226.00	6
	Controls	83.00	6	124.83	6	174.33	6	215.80	5	237.40	5	262.20	5
All	Tests	83.86	15	128.00	15	166.50	14	198.07	14	228.33	12	245.70	10
	Controls	81.81	16	131.81	16	166.37	16	207.50	14	236.50	14	258.00	13

females were less often pregnant than the controls; they produced less than half as many litters, while the offspring of the treated females produced nearly half as many again as their controls (MACDOWELL 1921). Supposing the larger the number of pregnancies the greater the inaccuracy, the weights estimated for the pregnant females among the controls would be more inaccurate than the tests in one generation and those for the tests would be more inaccurate than the controls in the other. The only justification for presenting the data for the females at all is that up to maturity they are as accurate as the males and taken altogether they form the only available material for comparison with the males.

The ages chosen for study are: forty days, sixty days, ninety days, one hundred and twenty days, one hundred and fifty days, and one hundred and eighty days. Thirty days would be the logical age to start with, but in many cases the first weighing was not made till after this age. At this time rats are growing very fast; to extend the curve backwards even a few days at this time introduces a large amount of inaccuracy due both to the small size of the weights and to the steepness of the curves as well as to the introduction of personal opinion. Every rat was weighed before forty days so the weight at this age could be interpolated without the chance of personal bias. Many rats were carried considerably beyond one hundred and eighty days, but the number of rats was much smaller after this age and the growth, aside from the deposition of fat, was practically completed by this time.

RESULTS

Summaries of the data are presented in the form of averages, for the males and females separately, for the test and control rats in each of the four strains used and for all the strains together, for each of the six ages

TABLE 2

Averages of the weight per female rat in grams for the different strains separately and together in each of the four generations.

A. Treated females

STRAIN		40 DAYS		60 DAYS		90 DAYS		120 DAYS		150 DAYS		180 DAYS	
		Means	No.	Means	No.	Means	No.	Means	No.	Means	No.	Means	No.
A	Tests	65.53	26	105.92	26	125.50	20	156.37	16	172.46	15	179.30	13
	Controls	69.50	26	112.46	26	134.08	23	169.72	18	184.70	17	195.76	17
B	Tests	65.00	5	103.14	7	122.14	7	160.66	6	166.66	3	175.50	2
	Controls	66.80	5	107.00	7	143.00	7	182.00	5	180.50	2	210.00	2
C	Tests	63.65	23	98.95	23	124.19	21	157.53	13	173.83	12	190.27	11
	Controls	65.09	22	108.86	22	138.00	19	182.38	13	188.00	11	205.72	11
L	Tests	64.27	11	105.54	11	117.87	8	145.71	7	157.25	4	182.00	2
	Controls	68.30	10	112.50	10	131.10	10	165.33	6	174.33	3	194.50	2
All	Tests	64.61	65	103.18	67	123.50	56	155.57	42	170.64	34	183.53	28
	Controls	67.55	63	110.66	65	135.89	59	174.47	42	184.60	33	200.00	32

B. Untreated females from treated parents

A	Tests	75.20	5	77.00	5	112.20	5	173.00	5	200.00	5	215.80	5
	Controls	63.50	4	78.75	4	107.00	4	161.50	4	192.25	4	208.50	4
B	Tests	71.33	6	81.33	6	101.33	6	146.16	6	167.16	6	175.66	6
	Controls	68.50	4	85.50	4	97.50	4	145.50	4	168.50	4	173.50	4
C	Tests	74.00	2	83.00	2	110.50	2	156.00	2	172.00	2	184.00	2
	Controls	58.33	3	67.66	3	91.00	3	152.00	3	179.00	3	188.00	3
L	Tests	64.22	9	89.55	9	96.33	9	154.55	9	182.77	9	190.44	9
	Controls	64.00	14	81.00	14	100.57	14	154.30	13	171.92	13	184.69	13
All	Tests	69.54	22	83.86	22	102.59	22	156.59	22	181.45	22	191.59	22
	Controls	63.96	25	79.76	25	99.96	25	153.75	24	175.62	24	187.20	24

C. Untreated females from untreated parents and treated grandparents

A	Tests	84.00	1	91.00	1	120.00	1	176.00	1	201.00	1	195.00	1
	Controls	86.00	3	120.00	3	138.60	3	182.30	3	216.60	3	220.00	3
C	Tests	60.00	2	79.50	2	100.00	2	139.00	2	167.00	2	.....	...
	Controls	76.00	2	72.50	2	76.50	2	140.50	2	180.00	2	184.00	2
L	Tests	62.85	7	99.00	7	100.14	7	126.57	7	149.43	7	182.66	6
	Controls	57.00	2	81.70	7	93.20	7	102.20	7	135.20	7	171.50	7
All	Tests	64.40	10	94.30	10	102.10	10	134.00	10	158.10	10	184.42	7
	Controls	74.85	7	85.25	12	101.88	12	128.66	12	163.08	12	182.63	11

TABLE 2 (continued)

D. Treated females from treated parents

STRAIN		40 DAYS		60 DAYS		90 DAYS		120 DAYS		150 DAYS		180 DAYS	
		Means	No.	Means	No.	Means	No.	Means	No.	Means	No.	Means	No.
C	Tests	74.00	9	110.11	9	138.33	6	166.60	5	183.25	4	201.50	4
	Controls	68.00	11	106.75	12	125.25	12	162.88	9	176.66	9	184.44	9
L	Tests	73.14	7	103.42	7	129.28	7	153.16	6	160.66	3	170.66	3
	Controls	70.71	7	100.85	7	134.42	7	158.83	6	175.25	4	179.33	3
All	Tests	73.62	16	107.18	16	133.46	13	159.27	11	173.57	7	188.28	7
	Controls	69.05	18	104.57	19	128.63	19	161.26	15	176.23	13	183.16	12

TABLE 3

Differences between the average weights of the tests and controls when the strains in each generation are taken together; when the average of the controls is greater, the difference is given a plus sign (+).

AGE	TREATED RATS		PARENTS TREATED		GRANDPARENTS TREATED		TREATED FROM TREATED PARENTS	
	Differences	Diff. / P. E.	Differences	Diff. / P. E.	Differences	Diff. / P. E.	Differences	Diff. / P. E.
	Males		Males		Males		Males	
40	+ 2.52±1.40	1.8	− 9.21±2.37	3.8	+ 4.67± 5.08	0.9	− 2.05±2.37	0.7
60	+12.69±2.16	5.9	−11.40±2.56	4.4	−13.98± 5.36	2.6	+ 3.81±3.81	1.0
90	+27.00±.316	8.5	− 9.47+3.64	2.6	− 5.64±11.64	0.5	− 0.13±4.96	0.0
120	+37.61±4.07	9.2	−13.12±5.13	2.5	−20.33±16.66	1.2	+ 9.43±6.01	1.5
150	+42.58±4.81	8.8	−10.54±6.24	1.6	−18.09±16.20	1.1	+ 8.17±6.48	1.2
180	+38.46±5.11	7.5	−10.15±7.61	1.3	− 5.34±13.52	0.4	+12.30±7.44	1.6
	Females		Females		Females		Females	
40	+ 2.94±1.16	2.5	− 5.58±2.36	2.3	+10.45±4.25	2.4	− 4.57±1.99	2.3
60	+ 7.48±1.63	4.6	− 4.10±2.35	1.7	− 9.05±3.21	2.8	− 2.61±3.04	0.8
90	+12.39±4.67	2.6	− 2.63±2.80	0.9	− 0.22±5.10	0.0	− 4.83±3.30	1.4
120	+18.90±2.97	6.3	− 2.84±2.94	0.9	− 5.34±7.87	0.6	+ 1.99±3.62	0.5
150	+13.96±3.26	4.3	− 5.83±3.38	1.7	+ 4.98±8.20	0.6	+ 2.66±4.35	0.6
180	+16.47±3.53	4.6	− 4.39±3.41	1.3	− 1.79±4.95	0.3	− 5.12±5.64	0.9

studied (tables 1 and 2). The number of rats included in each average is indicated in the column immediately following it; just below each test average is placed the corresponding control average. Four generations are given: (1) treated rats (the first ones treated); (2) their children (untreated from treated parents); (3) their untreated grandchildren (untreated from untreated parents and treated grandparents); (4) children of treated rats that were themselves treated (treated from treated parents). All the averages are shown graphically in figures 1 and 3; the broken lines

represent the tests (treated rats or their descendants), the solid lines the controls in the respective generations and strains. The ages in days are shown on the base lines and the ordinates represent the weights in grams.

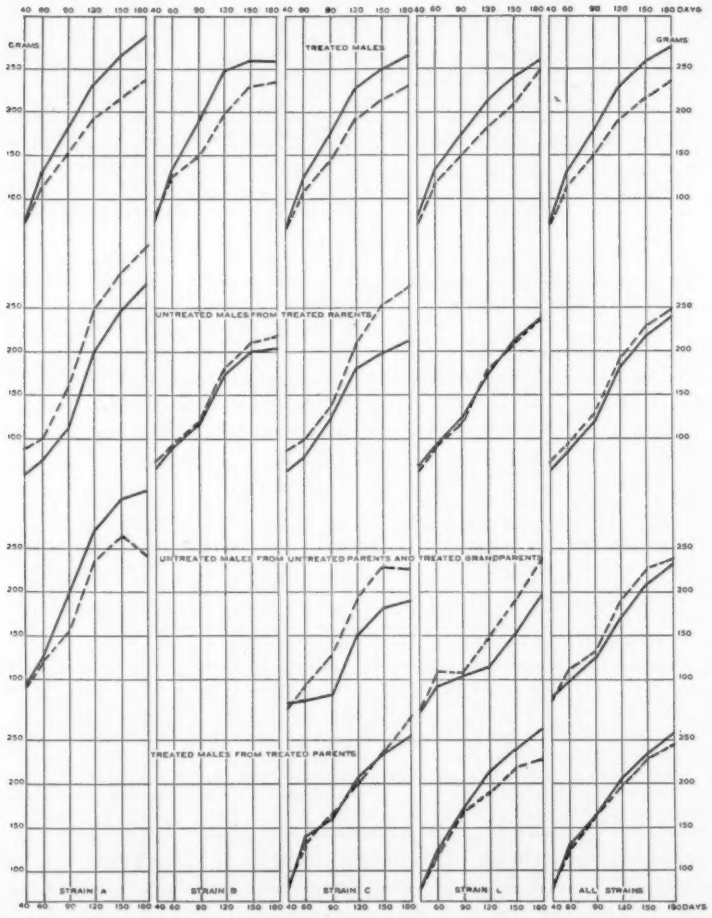

FIGURE 1.—Growth curves of the test and control males, plotted from the data given in table 1. The broken lines represent the tests (treated rats or descendants of treated rats), the solid lines the controls. The curves in the same vertical column belong to the same strain; the column at the right includes all strains; the horizontal rows of curves represent the different generations.

The curves are arranged in the chart so that the different generations of one strain lie in the same vertical column; in the column at the right the averages (primary averages, not averages of strain averages) for all strains together are shown. All the curves, those for the test rats as well as for the controls, are lower at ninety days than they normally should be, due to the light feeding that was administered in connection with the maze training that was being given to both groups at this time.

Treated rats

A part of the weight data from treated males has already been presented (MACDOWELL and VICARI 1917) in a preliminary report; the addition of more data in the present report does not change the earlier conclusions. The treated males grow less rapidly than the controls. This is true whether the strains are considered separately or together. At forty days the weights are very nearly equal, although in strains C and L controls are already higher than the tests. The data available for thirty days indicate that the weights for this time were alike for the two groups. This is the result of making a purely random division of the males and females in each litter into two groups, those to be treated and those to be used as controls. Table 3 gives the differences between the averages for the treated rats and their controls when all strains are taken together. With the exception of the first comparison (at 40 days) all ages give differences that are unquestionably significant; the smallest of these, occurring at 60 days, is 5.9 times the probable error, three times the probable error being the recognized criterion of statistical significance. The frequency distributions of the individual weights of the males, all strains taken together, are given in figure 2. There is a pair of frequency polygons for each age. Beginning with forty days in the lower left-hand corner, the successive curves give the distributions for 60, 90, 120, 150, and 180 days. With the exception of the pair for 40 days, these curves are plotted on a percentage basis; the small amount of variation in the weights at 40 days has led to the use of classes half as wide in classifying these data. In order to compensate for this and make the actual area included by the curves equal to the others they have been plotted on the basis of two hundred instead of percent. The base lines are scales of weight in grams and all the curves are drawn on the same continuous scale; the numbers given are the lower limits of the respective classes. The vertical scales are the proportions in each weight class of the total number of individuals. Although there is very little difference between the distributions of the treated rats and their controls at forty days, a tendency is

already suggested for the treated rats to be lighter; there is a smaller proportion of the treated rats in classes of 80, 90 and 100 grams and a larger proportion of them in classes of 60 and 70 grams. At sixty days this tendency is more marked; the proportion of treated rats in classes of 80, 100 and 120 grams is greater than the controls in these classes, but there is a higher proportion of controls in classes of 140 and 160 grams.

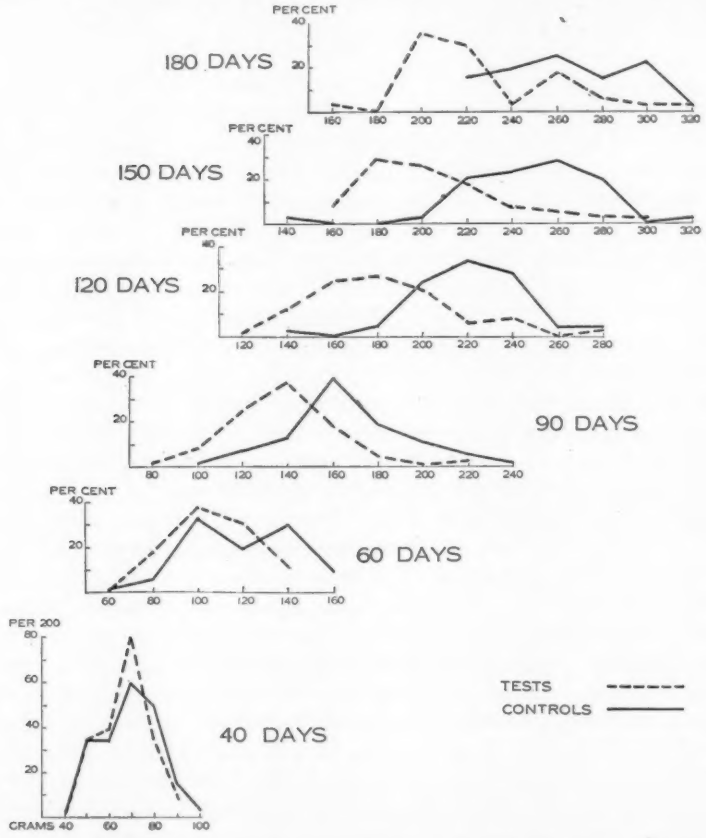

FIGURE 2.—Frequency distributions of the weights of the treated males at the different ages. The broken lines are the tests and the solid lines the controls; all curves are drawn on the same scale of weights, but the frequency scale is repeated for each pair of curves. All frequencies are in percents but those for forty days, which are given per 200, as the class width for 40 days is half the size of the others.

At 90 days the curve of the treated rats has drawn well away from that of the controls so that the two modes fall in separate classes. The curves cross between the classes of 140 and 160 grams; below the point of crossing there is a higher proportion of treated rats in each class; above the point of crossing there is a higher proportion of controls. By 120 days the modes of the two distributions are two classes apart, with greater differences on

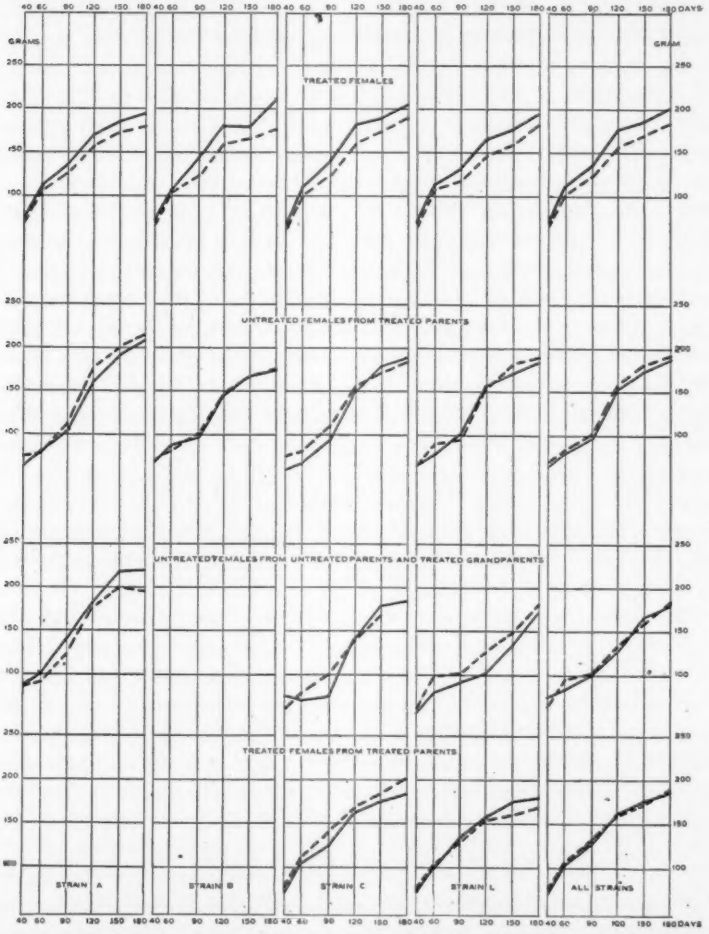

FIGURE 3.—Growth curves of the test and control females plotted from the data given in table 2. The broken lines represent the tests, the solid lines the controls.

either side of the crossing point. By 150 days the modes are five classes apart. The numbers are smaller at 180 days and this shows in the irregularity of the curves. There is only a little advance in weight over the 150-day distributions as a whole, but the concentration of the treated rats below the mass of controls is clearly more marked. During this progressive separation of the two distributions there have remained a few treated rats as heavy as the heaviest controls, but there can be no doubt that a real lowering of the treated group as a whole has occurred. The results given by the averages are not due to some erratic distribution of a few individuals but to the general movement of the population as a whole. Turning to figure 3, which gives the results for the females corresponding to the males in figure 1, the averages for treated females are found in the first row of curves. These curves are plotted on the same scale as those for the males and may be compared directly; the ruling of the background is also the same for both figures, and the strains given in the same order. The first thing to attract attention is that the females do not grow so fast as the males and by 180 days they are considerably lighter,—a well known fact but one sometimes not taken into account. Compared with their untreated sisters (controls) the treated females average lower at each age. At forty days the difference has already appeared in each strain, although like the males, they were probably equal at thirty days. For the later ages the absolute differences between the averages of the treated and control females are not as great as they are for the males. Table 3 shows that, when all strains are taken together, the differences are more than four times their probable errors for the ages of 60, 120, 150 and 180 days, and over twice their probable errors for the ages of 40 and 90 days.

The general conclusion may be stated: The treatment of white rats with maximum doses of alcohol by the inhalation method tends to reduce the rate of growth of the treated animals as compared with their untreated sibs raised at the same time and under the same conditions. This appears in the averages and the distributions but it does not affect all individuals alike, since some remain as heavy as the heaviest controls. In spite of the smaller absolute differences and the unreliability occasioned by their pregnancies, the females give the same general results as the males.

Untreated rats from treated parents

The second row of curves in figures 1 and 3 shows the averages of the weights of the offspring resulting from matings between the treated males and treated females (sisters by brothers) and between the controls (sisters by brothers).

In this and the following generations all the rats were trained in a multiple-choice apparatus as well as in the maze; this occasioned a continuation of the light feeding for a longer time, so that the weights for 120 days as well as for 90 days are lower than they would be normally. The males from treated parents in strains A and C have higher averages than the controls at all ages; the same difference is present in strain B, although not so strongly marked. In strain L there is no difference between the curves for the tests and controls. When the four strains are combined parallel curves result, with the tests heavier throughout. Table 3 indicates that the differences are probably statistically significant for the first three ages (being 3.8, 4.4, 2.6 and 2.5 times their respective probable errors), but for the last two ages they are not significant. The females in this generation show less consistent results, but the tendency for the tests to be heavier than the controls appears in strains A and C; and when all the strains are put together, the test and control curves are parallel, with the tests heavier than the controls at all ages. The differences are so small, however, that, in comparison with their probable errors (see table 3) they can not be considered statistically significant. In spite of this, the direction of the differences and their consistency in the different ages support the conclusion warranted by the results from the males, that the offspring of the treated rats tend to be heavier than the offspring from the controls.

Untreated rats from untreated parents and treated grandparents

This generation was produced by inbreeding rats in the preceding generation, the tests by their own sibs and the controls by their own sibs. Strain B was not carried to this generation. The numbers raised, as indicated in table 1, are very small. For the males in strains C and L the test averages are heavier than the controls; strain A, on the other hand, shows the controls heavier than the tests (see third row of curves in figures 1 and 3). The females also show the controls heavier in strain A and the tests in strain L, but in strain C there is no consistent difference between the tests and controls. When all strains are put together the averages show the test males higher than the controls and practically no difference at all between the test and control females. At 60 days the differences for both males and females are in favor of the tests and they are probably statistically significant, being 2.6 and 2.8 times their probable errors; the only other difference that approaches three times its probable error is for the females at 40 days when the control average is higher, the difference being 2.4 times its probable error.

No definite conclusion can be drawn from such results. The numbers are too small, in the absence of consistency in the different strains and the sexes, to prove anything; but, as far as any general difference between the tests and controls is indicated, it appears to be in favor of the tests.

Treated rats from treated parents

Some of the rats in strains C and L produced by the first treated generation were themselves given the treatment. This treatment was started when the animals were weaned; it was given full strength at once, that is, without any preliminary lighter treatment, the rats were immediately left in the fumes each day until they became dead drunk. Weights are given for thirty-one animals so treated and thirty-four controls. As far as their breeding is concerned these rats are comparable with the untreated rats from treated parents whose weights are represented in the second row of curves in figures 1 and 3. The curves (the bottom row in figures 1 and 3) show that the test males in strain C were almost exactly equal to the controls; the test females in this strain were slightly heavier than the controls. In strain L the test males were slightly lower than the controls in the later ages, but the test females barely suggest a similar lowering of the tests at the ages of 150 and 180 days. With the strains taken together, there appears to be no general difference in either sex between the tests and controls; none of the differences found at individual ages is significant.

DISCUSSION

Reviewing the results in all the different generations, the following statements may be made: Treating rats with strong doses of alcohol fumes tends definitely to reduce the rate of their growth, but the untreated offspring of such treated rats tend to be heavier than the controls. Although no generalization can be made for the grandchildren of the treated rats, the small number of data at hand suggest that they too tend to be heavier than the controls. While the treatment of one generation reduces the rate of growth, the treatment of rats from treated parents seems to have no effect at all upon the rate of their growth.

Taken by themselves such results appear to be inconsistent and unsatisfactory, but taken in connection with the results of the study of the fertility of these same rats and in the light of PEARL'S (1917) suggestion of the selective effect of alcohol, they are not at all surprising. It has been shown (MACDOWELL 1921) that the treatment of these rats reduced the expected number of litters. Compared with the untreated sibs, the treated rats

failed to produce over 64.8 percent of the litters expected, but the offspring they did raise in turn gave birth to 33.3 percent *more* litters than the controls in the same time. These are definite results and they give a clear indication of how the data are to be interpreted. It is only necessary to suppose a certain amount of correlation between weight and the ability to produce litters, to understand how the alcohol could reduce the weights in one generation and cause an increase over the controls in the next generation. If the alcohol should prevent certain females from having any litters and these females were the ones carrying genes for lighter weight as well as poorer reproductive capacity, the offspring that were produced would be a selected lot as compared with the controls, and they would bear fewer genes for infertility and fewer for light weight, supposing these genes are different. The generations following should still show the superiority of the descendants of the treated rats. The fertility data show this clearly in spite of the small numbers, but the weight data are too variable to give clear results. For the males there did appear to be a slight tendency for the tests to average higher.

If the application of alcohol to one generation reduces the rate of growth, why does not the treatment of the offspring as well cause a reduction in weight as great or greater? The facts are clear that such a reduction in the weights of treated offspring is not found, and equally clear that the treatment of the first generation has the immediate effect of reducing the rate of growth in most rats. The lack of modification found when the treated rats came from treated parents can be explained by supposing them to be a selected lot superior genetically to the controls, so the treatment may reduce their potential weight and yet leave them no lighter than the controls. This is the result to be expected when the immediate somatic tendency of the alcohol to reduce weight, and its indirect genetic tendency to cause an increase in weight are both working upon the same animals.

RELATED INVESTIGATIONS

In spite of the vast literature on alcoholism, there are very few papers giving experimental results of the effect of alcohol on the growth of animals. For purposes of comparison certain of these will be cited. ARLITT (1919) reported weighing white rats that were treated with alcohol, as well as their descendants. She concluded (p. 10) that,

> "In all cases alcohol causes a marked retardation in the rate of growth as judged by the disparity in body weight of alcoholics as compared with normals of the same age. Parental alcoholism has a more marked effect on the rate

of growth than is present when the drug is administered to the animals themselves, as is obvious from analysis of the growth curves shown in figure II."

In the third and fourth generations this retardation in weight is present to a slightly less degree. "The defective body weight acquired by alcoholized rats is also inherited" (p. 12). In spite of this sweeping claim to have proved the inheritance of an acquired character, no critical estimation of any of these conclusions is possible. The data are presented in the form of curves, with no indication of the number of animals involved, with no apparent recognition of the sexual difference in weight, and with no information as to the genetic or environmental qualifications of the controls. A careful study reveals the fact that the same control data are used for comparison with each of the four generations, although this is obscured by the use of three different scales in plotting the four generations.

STOCKARD and PAPANICOLAOU (1917) give data from guinea-pigs on the birth weights and weights at the end of the first and third months. The summaries would seem to indicate that normal offspring weigh more, and shortly after birth, grow more rapidly than the young of alcoholic guinea-pigs. A complicated relationship is shown between the birth weights and growth and the number in the litter. Since small litters tend to have heavier offspring, and since the test animals tend to have smaller litters, the apparent effects of alcohol are minimized. There is no separation of the data on the basis of the number of generations from treatment.

NICE (1912) reported that alcohol fed to adult white mice had a fattening effect upon them; they grew heavier than the controls. The treated offspring of these treated adults also surpassed the controls but the untreated offspring from the same parents grew faster still. Unfortunately the controls were probably not genetically comparable; all the mice first treated were secured "from a dealer and guaranteed not to be brothers and sisters," and when those originally chosen as controls proved to be unsatisfactory breeders, others were obtained "from the same source as the first lot of mice so as to serve as controls for comparison with the second generation of other lines." In view of these facts, the comparisons between the treated rats and their controls have very uncertain significance. On the other hand, the comparison of treated offspring with untreated offspring from the same parents is not open to the same uncertainty, since the probability of genetic similarity between the two sets is greatly increased. This comparison shows that, parentage being equal, mice treated with alcohol from the age of three weeks are lighter than

their untreated brothers and sisters. This is the one case in which treatment was begun before the animals were adult; it is accordingly comparable with the experiments herein reported and gives the same general result as far as it goes.

Later, NICE (1917) repeated these experiments: "the white mice given alcohol by the inhalation method gave much the same results as those that received it in their food in my former experiments" (p. 606). It should be noted however that the whole stock of mice used in this experiment came from the same known strain so that the controls were more comparable than in the first experiment, and instead of growing more rapidly, the first mice treated (started when 11 weeks old) gained weight less rapidly than the controls. The offspring of the treated mice grew faster than the controls, as was the case with the rats in the present experiment, but their superiority over the controls seemed to be maintained whether further treatment was given or not. In connection with a study of the effects of alcohol upon the acitivity of mice, NICE (1913) gave further data on weight. Records of four treated mice and four controls are given. Qualitatively these controls seem to be more satisfactory than any others that have been presented for the study of the immediate effects of alcohol; they were all of the same sex and closely related; however the dosage was very light, consisting of 3 cc of 35 percent alcohol given with the food every other day, and 35 percent alcohol instead of water to drink, and the treatment did not begin till the mice were practically grown at 8 weeks. In ten of the eleven weighings that were made the control averages were higher, but at the beginning of the experiment the controls averaged 1.16 grams higher than the treated mice, and this difference is not exceeded at any other age but the last (36 weeks) when two of the four treated mice had died. If this has no other significance, it shows that the supposition that alcohol has a general tendency to fatten does not hold.

In comparing the growth curves of fowl treated with ethyl and methyl alcohol with those of the untreated birds, PEARL (1917) found that no "profound or far-reaching effect upon the general metabolic processes of these birds has as yet been produced by the treatment" (p. 175). This conclusion is based on 15 monthly weighings of 14 treated birds (10 hens and 4 cocks) and four weighings of the controls (supposedly 39 hens). The treated hens are heavier than the controls between November and January of the first year and between September and January of the second year. From January to June there is a great reduction in the weight of the treated hens, but since there are no control data for this

period it cannot be proven that this drop is due to the treatment. However PEARL considers that this is probably the first significant effect of the administration of the alcohol. A full series of weights of the offspring of treated birds and controls is given from hatching to about three hundred days. The offspring of the treated birds tend to grow heavier than the controls, although this difference does not appear for three or four months after hatching.

SUMMARY

Data presented in this paper would seem to warrant the following conclusions:

1. Treatment of white rats with the fumes of alcohol from the time of weaning to maturity reduces the rate of growth as compared with that of their untreated brothers and sisters.

2. The untreated male offspring of treated rats are heavier on the average than the controls in this generation.

3. There is some indication of a slight tendency for the male grandchildren of the treated rats to be heavier than the controls in their generation.

4. The male offspring of treated rats that are themselves treated show no differences in weight from their controls.

5. In all cases the females give less reliable results than the males on account of the pregnancies, but in so far as they show anything they support the results based on the males alone.

6. These results may be interpreted by supposing that the alcohol treatment has two opposing tendencies, namely, (1) a tendency to retard the normal rate of growth, and (2) a tendency to prevent the reproduction of those females bearing weaker-growth genes and so to raise the weight average in the next generation.

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THE CORRELATION BETWEEN THE EGG PRODUCTION OF THE VARIOUS PERIODS OF THE YEAR IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL

J. ARTHUR HARRIS

Station for Experimental Evolution, Cold Spring Harbor, Long Island, New York

and

H. D. GOODALE

Massachusetts Agricultural Experiment Station, Amherst, Massachusetts

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INTRODUCTION

This paper has for its purpose the consideration of the correlation between the egg records of various periods of the year in the Rhode Island Red breed of domestic fowl. Such correlations have already been determined and are in part published for the White Leghorn breed (HARRIS, BLAKESLEE and WARNER 1917; HARRIS, BLAKESLEE, WARNER and KIRKPATRICK 1917; HARRIS, BLAKESLEE and KIRKPATRICK 1917, 1918). In the discussion of the present investigation, we shall assume a knowledge of the results of these earlier studies, particularly that on the correlation between the records of various periods in the White Leghorn (HARRIS, BLAKESLEE and KIRKPATRICK 1918).

In addition to the general biological importance of the knowledge of the interrelationship between the physiological activities of the organisms of a population at various periods, such as will result from the determination of these correlations, the investigations have a potential practical significance. The existence of a correlation between the records of the individ-

ual months and the record of the year as a whole is the basis upon which the possibility of the prediction of the record of groups of birds for longer periods from the measured record of a short period of time must rest. In the case of the White Leghorn fowl, such prediction has been shown to be possible with a high degree of accuracy[1] (HARRIS, KIRKPATRICK and BLAKESLEE 1921; HARRIS, KIRKPATRICK, BLAKESLEE, WARNER and CARD 1921). It is, therefore, important to determine whether correlations of a similar magnitude also exist in breeds other than the White Leghorn. The investigation of the correlation existing in an individual flock is also a matter of considerable practical interest. Our earlier correlations, both those deduced from the Storrs series (HARRIS and others, loc. cit.) and from the Vineland series (HARRIS and LEWIS 1921) were based upon series of birds which were submitted by widely scattered breeders. There is a possibility of the correlations deduced in these cases being considered as due to the heterogeneity of materials thus assembled. This point can be settled only by determining correlations for individual flocks and comparing these with correlations deduced from contest samples drawn from many flocks. It is evident that if the methods of prediction of egg production are to be commercially applied, the practical use must be made in individual flocks. It is, therefore, economically essential to determine whether correlations are found in individual flocks similar to those which have been demonstrated in contest series.

It must not be inferred that we are oblivious to the many biological factors, extrinsic as well as intrinsic, upon which fecundity depends. Certain of these factors, such as time of maturity and broodiness, have been especially emphasized by one of us (GOODALE 1918 a, b, 1920). The great labor of calculation renders it impossible to treat all of the variables simultaneously. The analysis must, therefore, proceed step by step. Ultimately we hope to study in greater statistical detail the interrelationship of the various factors which for the moment must be left out of account.

The present paper on the Rhode Island Red breed is one of a series to be devoted to the more important breeds. A general comparison of results is reserved until the detailed presentation of the constants for each of the breeds is completed.

[1] While it is possible to make predictions for groups of birds, which are highly accurate on the average, it must not be inferred that it is possible to apply these equations to the prediction of the production of specific individuals.

MATERIALS

The materials upon which this study is based are the egg records for the pullet year made by the Rhode Island Red flocks at the MASSACHUSETTS AGRICULTURAL EXPERIMENT STATION for the laying years 1912-1913 to 1918-1919. Records made by birds that died or became pathological are omitted. The foundation stock, 1912-1913, came mainly, but not exclusively, from a single breeder. In 1915-1916, considerable new blood was added. During the period under consideration, breeding experiments dealing with egg production were going on, but aside from this fact, the flocks are a fair sample of what might be obtained from trap-nest records on any commercial poultry farm of similar size. Every care has been taken to keep the daily records accurately and to maintain all controllable environmental factors uniform.

In order to secure as many checks as possible on the trustworthiness of the constants it has seemed desirable to treat the materials in three groups. We have, therefore, determined the correlations for the 443 birds of 1915-1916, for the 442 birds of 1916-1917 and finally for all the birds of the seven years.

PRESENTATION AND ANALYSIS OF DATA

The correlation between the record of the individual months and annual production

The correlation between the production of the individual months of the year and the annual egg record for the series for the two individual years, 1915-1916 and 1916-1917 appear in table 1. The correlations for the whole period, 1912-1919, are given in the first section of table 2.

It is clear that the correlations are of a substantial magnitude and statistically significant in comparison with their probable errors throughout. They are thus in full general agreement with the results obtained from the White Leghorn birds exhibited at the INTERNATIONAL EGG LAYING CONTEST at Storrs, Connecticut.

The constants indicate, therefore, that the production of any individual month should furnish a reasonably satisfactory basis for the prediction of the annual egg production of the Rhode Island Red fowl just as it has been shown to be in the case of the White Leghorn fowl.

It is interesting to note from the difference column in table 1 that the differences between the correlation coefficients deducted for the two different years are in general small. Five of them are less than twice as large as their probable errors. In view of the fact that less than five

TABLE 1

Correlation between the egg production of twelve individual months and total annual egg production.

MONTHS	CORRELATIONS		DIFFERENCE (1916-1917) −(1915-1916)	DIFF. / $E_{diff.}$
	1915-1916	1916-1917		
November	.3245 ± .0287	.4357 ± .0255	+.1112 ± .0384	2.90
December	.4887 ± .0244	.6646 ± .0179	+.1759 ± .0302	5.82
January	.5753 ± .0214	.5910 ± .0209	+.0157 ± .0299	0.53
February	.5092 ± .0237	.5937 ± .0208	+.0845 ± .0315	2.68
March	.5020 ± .0240	.5763 ± .0214	+.0743 ± .0321	2.31
April	.5522 ± .0223	.4427 ± .0258	−.1095 ± .0341	3.21
May	.5255 ± .0232	.4798 ± .0247	−.0457 ± .0353	1.29
June	.5395 ± .0227	.5460 ± .0225	+.0065 ± .0320	0.20
July	.5585 ± .0221	.5623 ± .0219	+.0038 ± .0311	0.12
August	.6021 ± .0204	.5522 ± .0223	−.0499 ± .0302	1.65
September	.5374 ± .0228	.6321 ± .0193	+.0947 ± .0299	3.17
October	.3978 ± .0270	.4979 ± .0241	+.1001 ± .0362	2.77

TABLE 2

Comparison of correlation between the egg production of the twelve individual months and total annual egg production in the Rhode Island Red and the White Leghorn breeds.

MONTHS	CORRELATIONS		DIFFERENCE (R.I.R.) −(W.L.)	DIFF. / $E_{diff.}$
	Rhode Island Red 1912-1913 to 1918-1919	Storrs White Leghorn 1911-1912 to 1916-1917		
November	.4678 ± .0130	.4040 ± .0132	+.0638 ± .0185	3.45
December	.5991 ± .0106	.5244 ± .0114	+.0747 ± .0156	4.79
January	.6349 ± .0099	.5062 ± .0117	+.1287 ± .0153	8.41
February	.5720 ± .0112	.5360 ± .0112	+.0360 ± .0158	2.28
March	.5553 ± .0115	.5769 ± .0105	−.0216 ± .0156	1.38
April	.4761 ± .0128	.5469 ± .0110	−.0708 ± .0169	4.19
May	.4401 ± .0134	.5904 ± .0102	−.1503 ± .0169	8.89
June	.5173 ± .0122	.6496 ± .0091	−.1323 ± .0152	8.70
July	.5361 ± .0118	.6711 ± .0086	−.1350 ± .0146	9.25
August	.5682 ± .0112	.6700 ± .0087	−.1018 ± .0142	7.17
September	.5940 ± .0107	.6526 ± .0090	−.0586 ± .0140	4.19
October	.4742 ± .0129	.5251 ± .0114	−.0509 ± .0172	2.96

hundred birds are involved in each series and that these birds have been subject to the differences in conditions of two years, the agreement may be considered excellent. This will be shown in another way later.

While a more detailed comparison between breeds is reserved until those other than the Rhode Island Red and the White Leghorn may be taken into account, it is interesting to compare in a wholly preliminary

way the results (hitherto unpublished) obtained from the data for White Leghorn birds as observed at Storrs during the six years 1911 to 1917. These are laid beside the series of Rhode Island Red birds observed at Amherst during the period 1912 to 1919 in table 2. The differences are in general much larger than those between the two series of Rhode Island Red birds compared above, and suggest that the two breeds may differ in their correlations. This furnishes an additional reason for the carrying out of a series of comparative studies on this problem.

For purposes of prediction we must pass from measures of interrelationship in terms of correlation to those expressed in terms of regression equations.

TABLE 3

Regression equations for the prediction of annual total egg production from monthly egg records.

MONTHS	REGRESSION EQUATIONS		
	1915-1916	1916-1917	1912-1913 to 1918-1919
November e_1	$E=116.853+2.174\ e_1$	$E=116.653+2.600\ e_1$	$E=118.050+2.794\ e_1$
December e_2	$E=108.366+2.406\ e_2$	$E=95.301+3.274\ e_2$	$E=106.027+2.987\ e_2$
January e_3	$E=97.114+2.695\ e_3$	$E=95.751+2.921\ e_3$	$E=95.609+3.104\ e_3$
February e_4	$E=91.093+2.551\ e_4$	$E=89.727+3.342\ e_4$	$E=88.828+3.249\ e_4$
March e_5	$E=66.974+3.079\ e_5$	$E=42.661+4.452\ e_5$	$E=58.396+3.880\ e_5$
April e_6	$E=50.253+4.062\ e_6$	$E=53.619+4.046\ e_6$	$E=60.015+3.895\ e_6$
May e_7	$E=61.579+3.832\ e_7$	$E=65.176+4.141\ e_7$	$E=73.194+3.579\ e_7$
June e_8	$E=74.667+3.915\ e_8$	$E=76.134+5.048\ e_8$	$E=78.474+4.233\ e_8$
July e_9	$E=84.414+3.920\ e_9$	$E=91.883+4.459\ e_9$	$E=90.035+3.903\ e_9$
August e_{10}	$E=87.999+4.046\ e_{10}$	$E=100.595+3.597\ e_{10}$	$E=94.704+3.929\ e_{10}$
September e_{11}	$E=101.996+3.076\ e_{11}$	$E=99.090+4.015\ e_{11}$	$E=101.666+3.754\ e_{11}$
October e_{12}	$E=113.621+2.574\ e_{12}$	$E=115.121+3.644\ e_{12}$	$E=116.928+3.402\ e_{12}$

This is essential not merely for purposes of testing the possibilities of prediction but for verifying the validity of the correlation coefficient as applied to the particular data in hand, the validity of the product-moment method of determining closeness of interrelationship depending upon linearity of regression.

The linear regression equations for the two years 1915-1916 and 1916-1917 appear in table 3. These equations are represented graphically in diagrams 1 to 3.

On these diagrams the results for the two years are laid side by side. The figures show: (1) a reasonable agreement of the results obtained for the two different years; and (2) a reasonable agreement of the empirical annual mean production of birds laying various numbers of eggs in

the individual months of the year with the fitted straight lines. Taking the series as a whole, the closeness of agreement, as judged by inspection, merely, would seem to be very comparable with that obtained from the two-years production of White Leghorn birds, submitted by a large num-

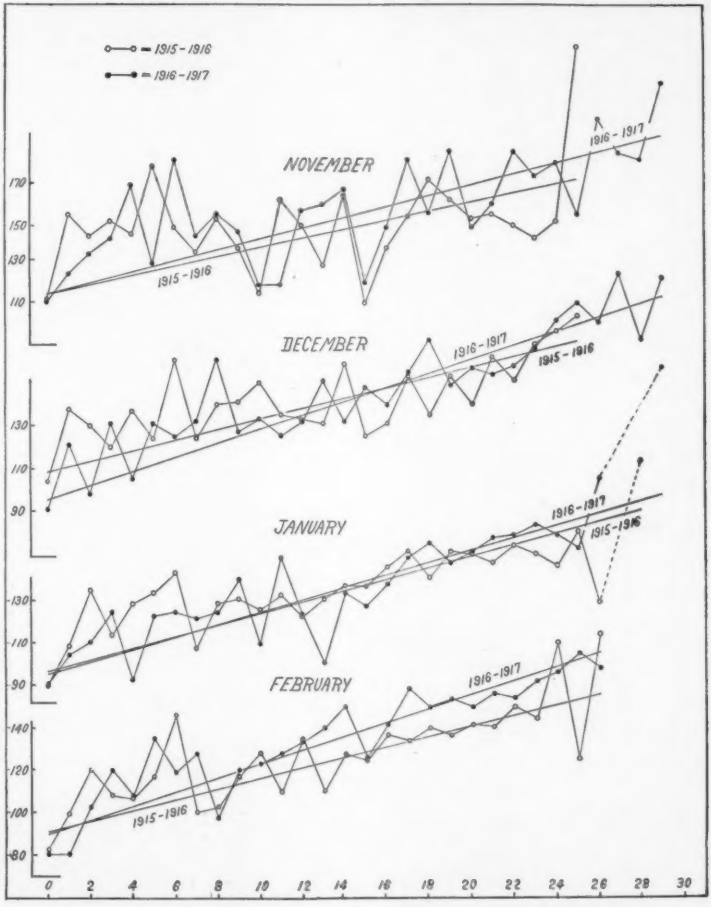

DIAGRAM 1.—Regression of annual production on monthly production.

ber of breeders in the INTERNATIONAL EGG LAYING CONTEST at Storrs (HARRIS, BLAKESLEE and KIRKPATRICK 1918, figures 2–5). While it can not be asserted that regression is strictly linear, these results indicate

unmistakably that prediction of the annual record of the Rhode Island Red fowl might be made with a relatively high degree of precision from the recorded performance of any individual month, just as has been shown to be possible in the case of the White Leghorn breed (HARRIS, KIRKPATRICK, BLAKESLEE, WARNER and CARD 1921).

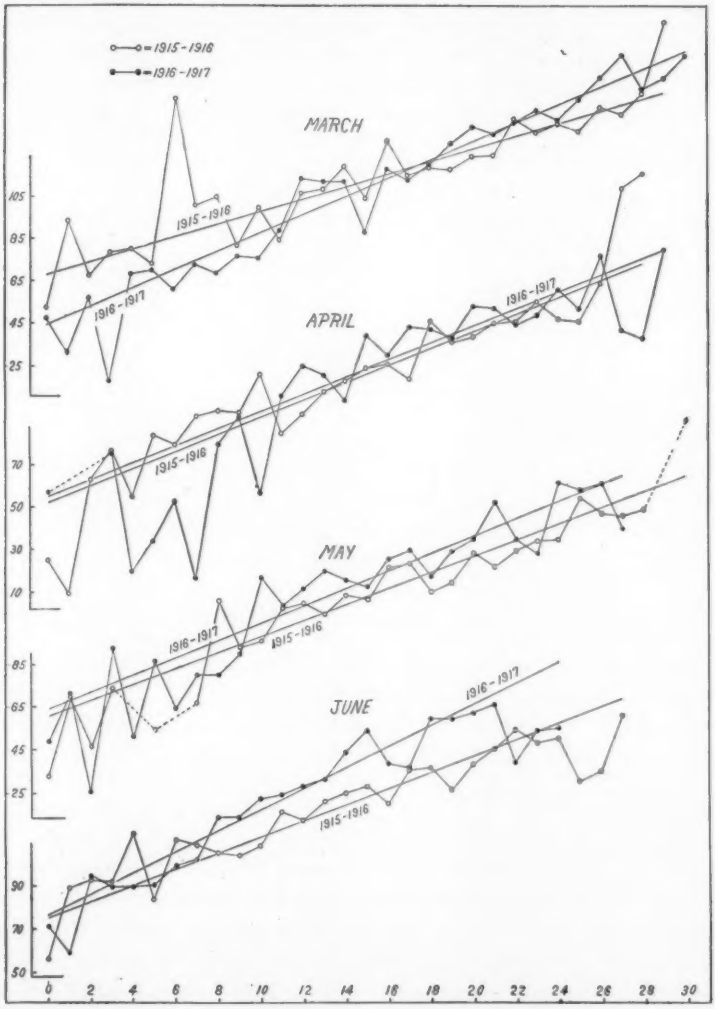

DIAGRAM 2.—Regression of annual production on monthly production.

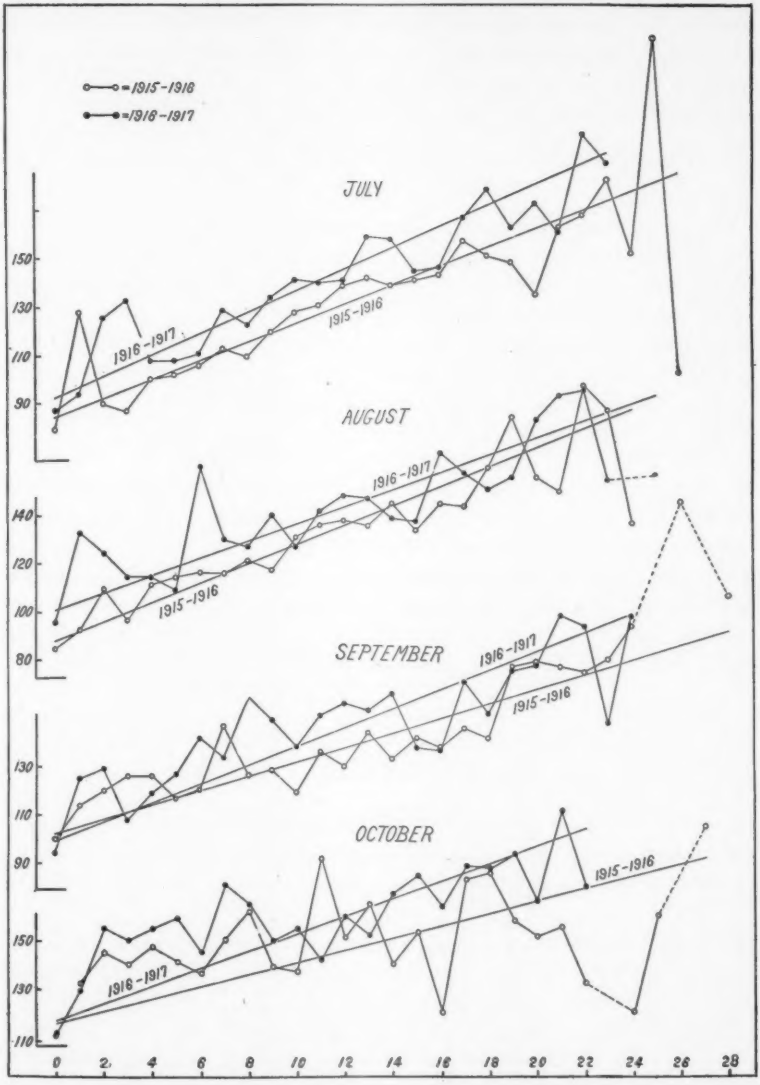

DIAGRAM 3.—Regression of annual production on monthly production.

The regression equations for the whole series of material, 1912 to 1919, are given in the final section of table 3.

These are not represented graphically in the present paper but will be given in a subsequent publication in which the results for Rhode Island Red birds studied in two different localities will be compared.

The correlation between the record of the individual month and that of the other eleven months of the year

Because of the fact that the production of each individual month of the year is included in the annual total production, the correlations between the productions of the individual months and the annual production must be expected to be positive in sign, and to some extent misleading as measures of the biological interrelationships between the different periods of the same year. This criticism will not apply to the correlations between the productions of the individual months and the total productions of the other eleven months of the year.

Calculating as we have in the White Leghorn series the correlation between the egg records of the individual months and the records of the remaining 11 months of the year, we obtain the results set forth in table 4.

These constants are lower throughout than those which have been deduced for the relationship between monthly production and annual production. This is shown clearly by diagram 4 in which the correlations for the production of each individual month and the production for the remaining 11 months of the year are compared with the correlations for

TABLE 4

Correlation between the monthly egg production and the record of the remaining eleven months of the year.

MONTHS	CORRELATIONS		
	1915-1916	1916-1917	1912-1913 to 1918-1919
November	.1822 ± .0310	.2990 ± .0292	.3218 ± .0149
December	.3110 ± .0289	.5256 ± .0232	.4456 ± .0133
January	.4046 ± .0268	.4341 ± .0260	.4866 ± .0127
February	.3385 ± .0284	.4593 ± .0253	.4347 ± .0135
March	.3649 ± .0279	.4797 ± .0247	.4441 ± .0133
April	.4467 ± .0257	.3484 ± .0282	.3733 ± .0143
May	.4153 ± .0265	.3831 ± .0274	.3330 ± .0148
June	.4306 ± .0261	.4632 ± .0252	.4192 ± .0137
July	.4483 ± .0256	.4665 ± .0251	.4271 ± .0136
August	.4937 ± .0242	.4314 ± .0261	.4577 ± .0131
September	.3951 ± .0270	.5223 ± .0233	.4763 ± .0128
October	.2563 ± .0299	.3846 ± .0273	.3554 ± .0145

these months and the annual production. The result shows, however, that the correlation between the individual months of the year and the annual total is not due primarily to the inclusion of the individual month in the second variable of the correlation. The constants show clearly that birds which are superior in any individual month of the year, also, on the average, show superiority in the other 11 months of the year.

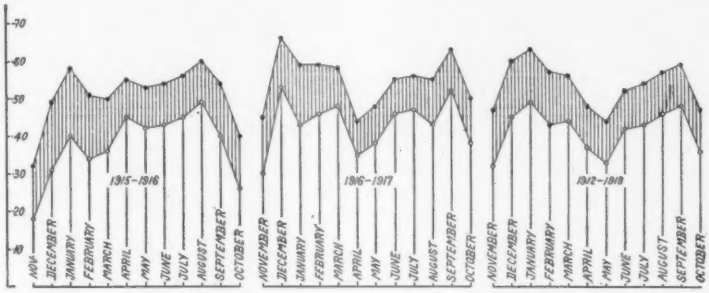

DIAGRAM 4.—Comparison of correlation between monthly production and annual production (solid dots) and between monthly production and the production of the remaining eleven months of the year (circles).

The correlation between the annual production and the deviation of the productions of the individual months from their probable values

In a study of the White Leghorn fowl (HARRIS, BLAKESLEE and KIRKPATRICK 1918, p. 46–49) the value of a coefficient showing the relationship between a variable and the deviation of a dependent variable from its probable value (HARRIS 1909) as a means of analyzing the interrelationship between the records of major and minor periods has been demonstrated.

The correlations between the annual record of the birds and the deviations of the contributions of the individual months to this annual record from their probable value appear in table 5 and are represented graphically in diagram 5.

These constants are also in excellent general agreement with those obtained from the first-year performance of the White Leghorn breed as exhibited at Storrs. The correlations show that November, December, January, February, August, September and October make relatively larger contributions to the annual production of superior birds than might be expected from the average results for the flocks as a whole. March, April, May and June make relatively far smaller contributions

to the annual production of highly superior birds than might be expected from the average records. The relation of July production to annual

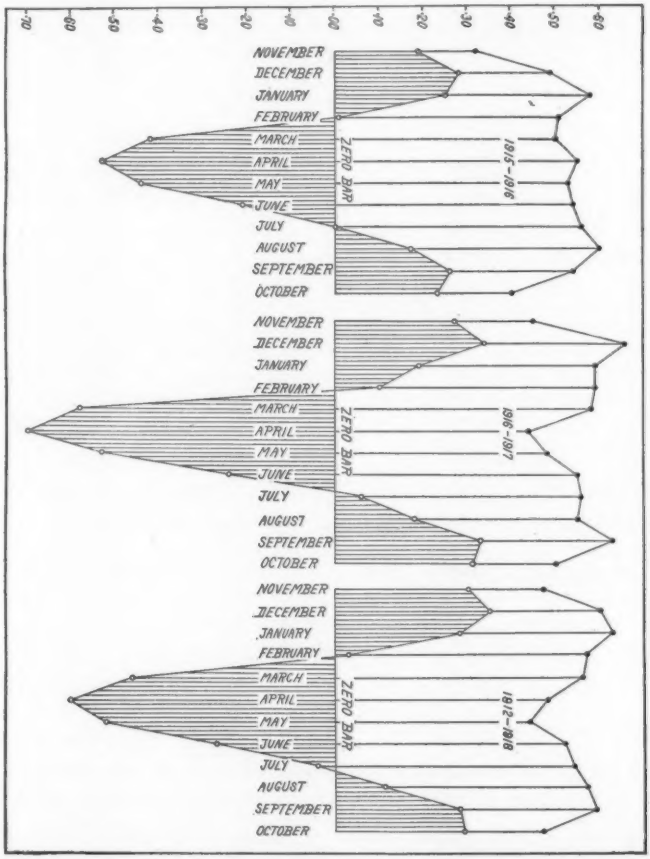

DIAGRAM 5. Correlation between annual production and monthly production (solid dots), and correlation between annual production and the deviation of monthly production from its probable value.

production is somewhat questionable since it falls sometimes in one category and sometimes in the other.

While the coefficient for February is positive in all three series, it is numerically very small.

These results furnish another form of expression for the biological fact that during the months of March, April and May all birds are laying at about their maximum capacity. Large annual superiority cannot, therefore, depend primarily upon increased production in these months but must depend upon either precocious laying (November, December and January) or persistently continued laying (August, September and October), or upon both.

The correlation between the records of the individual months of the same year

Earlier studies (HARRIS and others, loc. cit.) have shown that in the White Leghorn there is a significant positive correlation between the records of each of five of the individual months of the first year and the records of each of the other eleven months of the first year. It has also been shown (HARRIS and LEWIS 1922) that there is in general a positive correlation between the records of the twelve individual months of the first year and the twelve individual months of the second year in the White Leghorn fowl.

TABLE 5

Correlation between annual egg production and the deviation of the monthly records from their probable value.

MONTH	CORRELATIONS		
	1915-1916	1916-1917	1912-1913 to 1918-1919
November	+.1893±.0309	+.2667±.0298	+.3003±.0151
December	+.2781±.0296	+.3439±.0283	+.3471±.0146
January	+.2543±.0300	+.1915±.0309	+.2766±.0153
February	+.0066±.0320	+.1027±.0317	+.0275±.0166
March	−.4205±.0264	−.5814±.0212	−.4623±.0131
April	−.5261±.0232	−.6986±.0164	−.5951±.0107
May	−.4433±.0258	−.5307±.0230	−.5211±.0121
June	−.2138±.0306	−.2350±.0303	−.2748±.0153
July	+.0021±.0320	+.0639±.0319	−.0386±.0166
August	+.1660±.0312	+.1841±.0310	+.1147±.0164
September	+.2587±.0299	+.3264±.0287	+.2770±.0153
October	+.2287±.0304	+.3125±.0289	+.2922±.0152

We have now to consider the possible correlations between the records of the individual months of the first year in the three groups of Rhode Island Red birds under consideration.

The constants appear in tables 6 and 7. In table 6 the upper entry of the group of three represents the correlation coefficient for the 442 birds studied in 1916-1917 while the second entry gives the correlation coefficient for the 443 birds studied in 1915-1916. The third entry gives the difference and the probable error of the difference between these two coefficients obtained by taking (1916-1917) − (1915-1916). In table 7 the first of the three entries gives the correlation coefficients for the 1658 birds representing the whole period 1912 to 1919. The second and third entries represent the differences between the correlation as deduced from this larger series and those derived from the series for 1916-1917 and 1915-1916, respectively. These differences are so taken that the sign shows whether the single-year series gives a larger (positive sign) or a smaller (negative sign) correlation.

We now have to consider the consistency in the correlations deduced for the two years. This may be tested in three ways. First, we may determine the difference in the average value of the possible correlations between the individual months of the year in the two years for which constants are available.[2] Second, we may compare the homologous constants individually with regard to their probable errors. Finally, we may determine the magnitude of the correlations between the homologous correlations in the two years.

Consider first the difference in the mean values of the two series. We have

For 1916-1917,	$.2448 \pm .0694$
For 1915-1916,	$.1960 \pm .0638$
Difference	$.0488 \pm .0275$

The average of the coefficients for 1916-1917 is slightly larger than that for 1915-1916, but the difference is only about twice as large as its probable error and cannot be asserted to be definitely significant.

For purposes of more critical comparison we must turn to the individual constants. The comparison of the individual coefficients for the two years has been made in table 6. Here the probable errors of the differences have been calculated in the usual manner.

It may be convenient to examine the frequency distribution of the differences. This is given in table 8. This shows that 19 of the 66 differences are negative, while 47 are positive in sign. This indicates clearly

[2] We deal with the correlations deduced for two individual years because we are not certain of the method of computing the probable error of the difference if the constants for the two individual years were compared with those for the whole period 1912 to 1919. It is for this reason that probable errors are not given for the differences in table 7.

TABLE 6

Correlations between the records of the individual months of the year

	NOVEMBER c_1	DECEMBER c_2	JANUARY c_3	FEBRUARY c_4	MARCH c_5	APRIL c_6	MAY c_7	JUNE c_8	JULY c_9	AUGUST c_{10}	SEPTEMBER c_{11}	OCTOBER c_{12}
November c_1		+.4509±.0256 +.5750±.0215 −.1241±.0334	+.0776±.0319 +.1332±.0315 −.0556±.0448	+.1685±.0312 −.0649±.0319 +.2334±.0446	+.1414±.0314 +.0202±.0320 +.1211±.0449	+.0935±.0318 +.0369±.0320 +.0566±.0451	+.1205±.0316 +.0347±.0320 +.0858±.0450	+.1507±.0314 +.0257±.0320 +.1250±.0448	+.1927±.0309 +.0664±.0319 +.1263±.0444	+.1299±.0315 +.0872±.0318 +.0427±.0448	+.1782±.0311 +.0303±.0320 +.1479±.0446	+.0801±.0319 −.0092±.0320 +.0893±.0452
December c_2	+.4509±.0256 +.5750±.0215 −.1241±.0334		+.5551±.0222 +.4763±.0248 +.0788±.0333	+.3604±.0279 +.0387±.0320 +.3217±.0425	+.2344±.0303 +.0930±.0318 +.1414±.0439	+.1005±.0318 +.0986±.0317 +.0019±.0449	+.1233±.0316 +.0382±.0320 +.0851±.0450	+.2023±.0308 +.0653±.0319 +.1370±.0443	+.2559±.0300 +.0418±.0320 +.2141±.0438	+.2104±.0307 +.0971±.0317 +.1133±.0441	+.2388±.0302 +.0966±.0318 +.1423±.0439	+.1970±.0308 +.0664±.0319 +.1306±.0444
January c_3	+.0776±.0319 +.1332±.0315 −.0556±.0448	+.5551±.0222 +.4763±.0248 +.0788±.0333		+.5704±.0216 +.4152±.0265 +.1552±.0342	+.2933±.0293 +.2220±.0305 +.0712±.0423	+.0257±.0321 +.1998±.0312 −.1341±.0448	+.0406±.0320 +.0704±.0319 −.0298±.0452	+.1183±.0316 +.0682±.0319 +.0501±.0449	+.1624±.0312 +.0839±.0318 +.0785±.0446	+.1312±.0315 +.1608±.0312 −.0296±.0444	+.1852±.0310 +.1364±.0315 +.0488±.0441	+.2424±.0302 +.1659±.0312 +.0764±.0434
February c_4	+.1685±.0312 −.0649±.0319 +.2334±.0446	+.3604±.0279 +.0387±.0320 +.3217±.0425	+.5704±.0216 +.4152±.0265 +.1552±.0342		+.4405±.0259 +.4206±.0264 +.0199±.0369	+.1350±.0315 +.2417±.0302 −.1066±.0436	+.0878±.0318 +.1285±.0315 −.0408±.0448	+.1681±.0312 +.0781±.0319 +.0900±.0446	+.1811±.0310 +.1049±.0317 +.0761±.0444	+.0880±.0318 +.1616±.0312 −.0737±.0446	+.1860±.0310 +.1554±.0313 +.0305±.0440	+.2366±.0303 +.1736±.0311 +.0630±.0434
March c_5	+.1414±.0314 +.0202±.0320 +.1211±.0449	+.2344±.0303 +.0930±.0318 +.1414±.0439	+.2933±.0293 +.2220±.0305 +.0712±.0423	+.4405±.0259 +.4206±.0264 +.0199±.0369		+.3185±.0288 +.3560±.0280 −.0375±.0402	+.3286±.0286 +.2021±.0307 +.1265±.0420	+.2873±.0294 +.1631±.0312 +.1241±.0429	+.2128±.0306 +.1610±.0312 +.0519±.0437	+.2510±.0301 +.1747±.0311 +.0764±.0432	+.2534±.0300 +.1078±.0317 +.1457±.0436	+.2031±.0308 +.1253±.0315 +.0778±.0441
April c_6	+.0935±.0318 +.0369±.0320 +.0566±.0451	+.1005±.0318 +.0986±.0317 +.0019±.0449	+.0257±.0321 +.1598±.0312 −.1341±.0448	+.1350±.0315 +.2417±.0302 −.1066±.0436	+.3185±.0288 +.3560±.0280 −.0375±.0402		+.4699±.0250 +.4819±.0246 −.0120±.0351	+.3563±.0280 +.3925±.0271 −.0362±.0390	+.2758±.0296 +.3053±.0291 −.0295±.0415	+.1939±.0309 +.2666±.0298 −.0727±.0429	+.2760±.0296 +.1943±.0308 +.0818±.0428	+.1841±.0310 +.0847±.0318 +.0994±.0444
May c_7	+.1205±.0316 +.0347±.0320 +.0858±.0450	+.1233±.0316 +.0382±.0320 +.0851±.0450	+.0406±.0320 +.0704±.0319 −.0298±.0452	+.0878±.0318 +.1285±.0315 −.0408±.0448	+.3286±.0286 +.2021±.0307 +.1265±.0420	+.4699±.0250 +.4819±.0246 −.0120±.0351		+.4612±.0253 +.5206±.0234 −.0595±.0344	+.3204±.0288 +.4193±.0264 −.0988±.0391	+.2622±.0299 +.3492±.0281 −.0870±.0410	+.3028±.0291 +.2201±.0305 +.0827±.0422	+.1603±.0313 +.0932±.0318 +.0672±.0446
June c_8	+.1507±.0314 +.0257±.0320 +.1250±.0448	+.2023±.0308 +.0653±.0319 +.1370±.0443	+.1183±.0316 +.0682±.0319 +.0501±.0449	+.1681±.0312 +.0781±.0319 +.0900±.0446	+.2873±.0294 +.1631±.0312 +.1241±.0429	+.3563±.0280 +.3925±.0271 −.0362±.0390	+.4612±.0253 +.5206±.0234 −.0595±.0344		+.4117±.0266 +.4605±.0253 −.0488±.0367	+.3206±.0288 +.4839±.0245 −.1632±.0378	+.3620±.0279 +.2958±.0292 +.0662±.0404	+.2120±.0306 +.0892±.0318 +.1228±.0442
July c_9	+.1927±.0309 +.0664±.0319 +.1263±.0444	+.2559±.0300 +.0418±.0320 +.2141±.0438	+.1624±.0312 +.0839±.0318 +.0785±.0446	+.1811±.0310 +.1049±.0317 +.0761±.0444	+.2128±.0306 +.1610±.0312 +.0519±.0437	+.2758±.0296 +.3053±.0291 −.0295±.0415	+.3204±.0288 +.4193±.0264 −.0988±.0391	+.4117±.0266 +.4605±.0253 −.0488±.0367		+.4122±.0266 +.5493±.0224 −.1371±.0348	+.3963±.0270 +.3799±.0274 +.0164±.0385	+.1502±.0314 +.1418±.0314 +.0084±.0444
August c_{10}	+.1299±.0315 +.0872±.0318 +.0427±.0448	+.2104±.0307 +.0971±.0317 +.1133±.0441	+.1312±.0315 +.1608±.0312 −.0296±.0444	+.0880±.0318 +.1616±.0312 −.0737±.0446	+.2510±.0301 +.1747±.0311 +.0764±.0432	+.1939±.0309 +.2666±.0298 −.0727±.0429	+.2622±.0299 +.3492±.0281 −.0870±.0410	+.3206±.0288 +.4839±.0245 −.1632±.0378	+.4122±.0266 +.5493±.0224 −.1371±.0348		+.5205±.0234 +.3942±.0271 +.1263±.0358	+.2813±.0295 +.1784±.0310 +.1029±.0428
September c_{11}	+.1782±.0311 +.0303±.0320 +.1479±.0446	+.2388±.0302 +.0966±.0318 +.1423±.0439	+.1852±.0310 +.1364±.0315 +.0488±.0441	+.1860±.0310 +.1554±.0313 +.0305±.0440	+.2535±.0300 +.1078±.0317 +.1457±.0436	+.2760±.0296 +.1943±.0308 +.0818±.0428	+.3028±.0291 +.2201±.0305 +.0827±.0422	+.3620±.0279 +.2958±.0292 +.0662±.0404	+.3963±.0270 +.3799±.0274 +.0164±.0385	+.5205±.0234 +.3942±.0271 +.1263±.0358		+.4205±.0264 +.3513±.0281 +.0692±.0386
October c_{12}	+.0801±.0319 −.0092±.0320 +.0893±.0452	+.1970±.0308 +.0664±.0319 +.1306±.0444	+.2424±.0302 +.1659±.0312 +.0764±.0434	+.2366±.0303 +.1736±.0311 +.0630±.0434	+.2031±.0308 +.1253±.0315 +.0778±.0441	+.1841±.0310 +.0847±.0318 +.0994±.0444	+.1603±.0313 +.0932±.0318 +.0672±.0446	+.2120±.0306 +.0892±.0318 +.1228±.0442	+.1902±.0314 +.1418±.0314 +.0084±.0444	+.2813±.0295 +.1784±.0310 +.1029±.0428	+.4205±.0264 +.3513±.0281 +.0692±.0386	

TABLE 7

Correlations between the records of the individual months of the year in the whole series, and comparison of these constants with those for two individual years.

	NOVEMBER c_1	DECEMBER c_2	JANUARY c_3	FEBRUARY c_4	MARCH c_5	APRIL c_6	MAY c_7	JUNE c_8	JULY c_9	AUGUST c_{10}	SEPTEMBER c_{11}	OCTOBER c_{12}
November c_1		+.5039±.0124 −.0530 +.0711	+.2044±.0159 −.1267 −.0711	+.1344±.0163 +.0340 −.1994	+.1399±.0163 +.0015 −.1196	+.0719±.0165 +.0216 −.0350	+.0365±.0166 +.0840 −.0018	+.0933±.0165 +.0575 −.0676	+.1495±.0162 +.0432 −.0831	+.1680±.0161 −.0381 −.0807	+.1724±.0161 +.0058 −.1421	+.1219±.0164 −.0418 −.1311
December c_2	+.5039±.0124 −.0530 +.0711		+.5597±.0114 −.0046 −.0835	+.2527±.0155 +.1076 −.2140	+.2262±.0158 +.0082 −.1332	+.1018±.0164 −.0013 −.0033	+.0338±.0166 +.0895 +.0044	+.0904±.0165 +.1119 −.0251	+.1208±.0164 +.1351 −.0790	+.1387±.0163 +.0717 −.0416	+.2027±.0159 +.0362 −.1061	+.1898±.0159 +.0072 −.1234
January c_3	+.2044±.0159 −.1267 −.0711	+.5597±.0114 −.0046 −.0835		+.5260±.0120 +.0444 −.1109	+.2943±.0152 −.0010 −.0722	+.1259±.0163 −.1002 +.0339	+.0405±.0166 +.0001 +.0299	+.0987±.0164 +.0196 −.0305	+.1382±.0163 +.0242 −.0543	+.1786±.0161 −.0474 −.0178	+.2357±.0157 −.0505 −.0994	+.2476±.0156 −.0052 −.0816
February c_4	+.1344±.0163 +.0340 −.1994	+.2527±.0155 +.1076 −.2140	+.5260±.0120 +.0444 −.1109		+.4212±.0137 +.0192 −.0006	+.2075±.0159 −.0724 +.0342	+.1061±.0164 +.0183 +.0225	+.1315±.0163 +.0366 +.0534	+.1378±.0163 +.0432 −.0329	+.1442±.0163 −.0562 +.0174	+.2075±.0159 −.0216 −.0521	+.1988±.0159 +.0378 −.0252
March c_5	+.1399±.0163 +.0015 −.1196	+.2262±.0158 +.0082 −.1332	+.2943±.0152 −.0010 −.0722	+.4212±.0137 +.0192 −.0006		+.3849±.0141 −.0664 −.0289	+.2439±.0156 +.0847 −.0418	+.2113±.0159 +.0760 −.0482	+.1594±.0162 +.0534 +.0016	+.2063±.0159 +.0447 −.0316	+.1934±.0160 +.0601 −.0856	+.1710±.0161 +.0321 −.0456
April c_6	+.0719±.0165 +.0216 −.0350	+.1018±.0164 −.0013 −.0033	+.1259±.0163 −.1002 +.0339	+.2075±.0159 −.0724 +.0342	+.3849±.0141 −.0664 −.0289		+.4399±.0134 +.0299 +.0420	+.3285±.0148 +.0278 +.0640	+.2414±.0156 +.0344 +.0639	+.2054±.0159 −.0115 +.0613	+.2032±.0159 +.0728 −.0090	+.1961±.0164 +.0780 −.0214
May c_7	+.0365±.0166 +.0840 −.0018	+.0338±.0166 +.0895 +.0044	+.0405±.0166 +.0001 +.0299	+.1061±.0164 −.0183 +.0225	+.2439±.0156 +.0847 −.0418	+.4399±.0134 +.0299 +.0420		+.4765±.0128 −.0153 +.0442	+.3570±.0145 −.0365 +.0623	+.2750±.0153 −.0128 +.0742	+.1897±.0160 +.1131 +.0304	+.0839±.0165 +.0774 +.0102
June c_8	+.0933±.0165 +.0575 −.0676	+.0904±.0165 +.1119 −.0251	+.0987±.0164 +.0196 −.0305	+.1315±.0163 +.0366 −.0534	+.2113±.0159 +.0760 −.0482	+.3285±.0148 +.0278 +.0640	+.4765±.0128 −.0153 +.0442		+.4561±.0131 −.0444 +.0044	+.3943±.0140 −.0736 +.0896	+.2972±.0151 +.0648 −.0013	+.1605±.0162 +.0515 −.0713
July c_9	+.1495±.0162 +.0432 −.0831	+.1208±.0164 +.1351 −.0790	+.1382±.0163 +.0242 −.0543	+.1378±.0163 +.0432 −.0329	+.1594±.0162 +.0534 +.0016	+.2414±.0156 +.0344 +.0639	+.3570±.0145 −.0365 +.0623	+.4561±.0131 −.0444 +.0044		+.4626±.0130 −.0505 +.0866	+.3568±.0145 +.0395 +.0231	+.1553±.0162 −.0051 −.0135
August c_{10}	+.1680±.0161 −.0381 −.0807	+.1387±.0163 +.0717 −.0416	+.1786±.0161 −.0474 −.0178	+.1442±.0163 −.0562 +.0174	+.2063±.0159 +.0447 −.0316	+.2054±.0159 −.0115 +.0613	+.2750±.0153 −.0128 +.0742	+.3943±.0140 −.0736 +.0896	+.4626±.0130 −.0505 +.0866		+.4387±.0134 +.0818 −.0445	+.2592±.0155 +.0221 −.0809
September c_{11}	+.1724±.0161 +.0058 −.1421	+.2027±.0159 +.0362 −.1061	+.2357±.0157 −.0505 −.0994	+.2075±.0159 −.0216 −.0521	+.1934±.0160 +.0601 −.0856	+.2032±.0159 +.0728 −.0090	+.1897±.0160 +.1131 +.0304	+.2972±.0151 +.0648 −.0013	+.3568±.0145 +.0395 +.0231	+.4387±.0134 +.0818 −.0445		+.4082±.0138 +.0123 −.0570
October c_{12}	+.1219±.0164 −.0418 −.1311	+.1898±.0160 +.0072 −.1234	+.2476±.0156 −.0052 −.0816	+.1988±.0159 +.0378 −.0252	+.1710±.0161 +.0321 −.0456	+.1961±.0164 +.0780 −.0214	+.0829±.0165 +.0774 +.0102	+.1605±.0162 +.0515 −.0713	+.1553±.0162 −.0051 −.0135	+.2592±.0155 +.0221 −.0809	+.4082±.0138 +.0123 −.0570	

that the series for 1916-1917 is slightly more highly correlated than that for 1915-1916. In further evidence of this fact we may note that these are only four groups, each of 0.05 range, of negative differences, wherear there are seven such groups of positive differences.

Considering the relation of the individual differences to their probable errors, as calculated by the usual formula, we have the frequency distribution shown in table 9. Here the frequencies of the various ratios to their probable errors are shown in groupings of unit range, the signs are those of the differences.

TABLE 8

DIFFERENCE IN CORRELATION (1916-1917) − (1915-1916)	FREQUENCY
−.151 to −.200	1
−.101 to −.150	4
−.051 to −.100	6
−.001 to −.050	8
+.001 to +.050	7
+.051 to +.100	21
+.101 to +.150	15
+.151 to +.200	1
+.201 to +.250	2
+.251 to +.300	
+.301 to +.350	1
Total	66

TABLE 9

RATIO TO PROBABLE ERROR AND SIGN OF DIFFERENCE	FREQUENCY
−4.001 to −5.000	1
−3.001 to −4.000	2
−2.001 to −3.000	4
−1.000 to −2.000	5
−0.000 to −1.000	7
+0.000 to +1.000	6
+1.001 to +2.000	19
+2.001 to +3.000	11
+3.001 to +4.000	7
+4.001 to +5.000	2
+5.001 to +6.000	1
+6.001 to +7.000	
+7.001 to +8.000	1
Total	66

We note that there are only five classes of negative ratios whereas there are eight classes of positive ratios. Again, it is clear that the frequency of large ratios is greater in the positive series. For example, there are only three cases in which the difference is over three times as large as its probable error in the negative differences, whereas there are eleven such cases in the positive differences. There are only seven cases in which the difference is more than twice as large as its probable error in the negative differences, whereas there are 22 such cases in the positive differences. It is clear, therefore, that the 1916-1917 series is somewhat more highly correlated than the 1915-1916 series.[3]

[3] There was less disease in the flock during 1916-1917, and the range conditions were better for the growing birds than in 1915-1916. This may, or may not, be the reason for the differences in correlation.

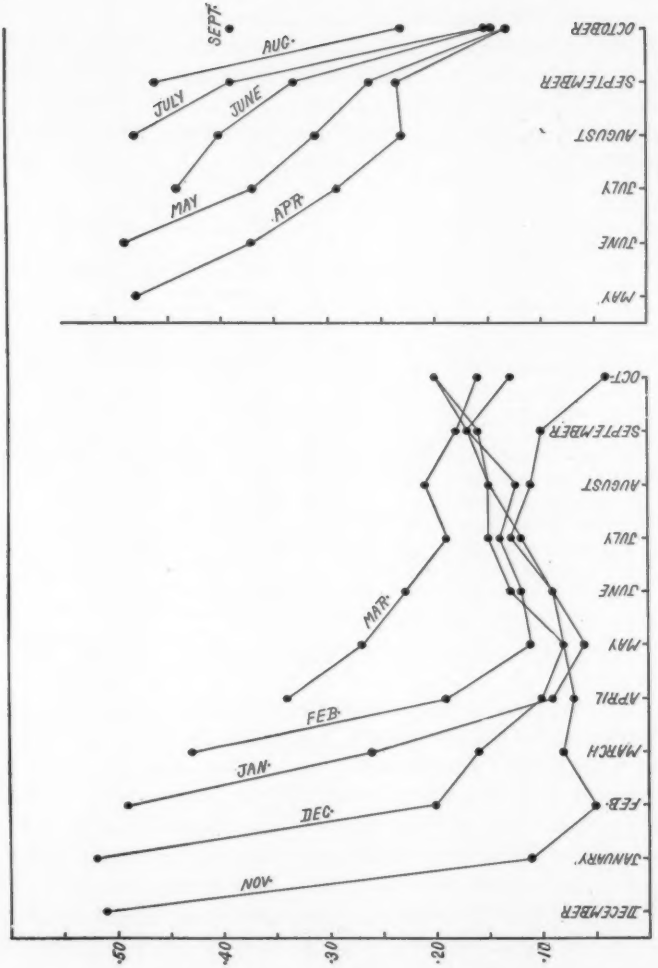

DIAGRAM 6.—Distribution of magnitudes of correlations between the records of individual months and the records of subsequent months of the same year.

The foregoing analysis demonstrates that the correlation between the individual months of the 1916-1917 series is on the whole slightly higher than that for the 1915-1916 series. As a measure of the general consistency of the two systems of coefficients we may determine the correlation

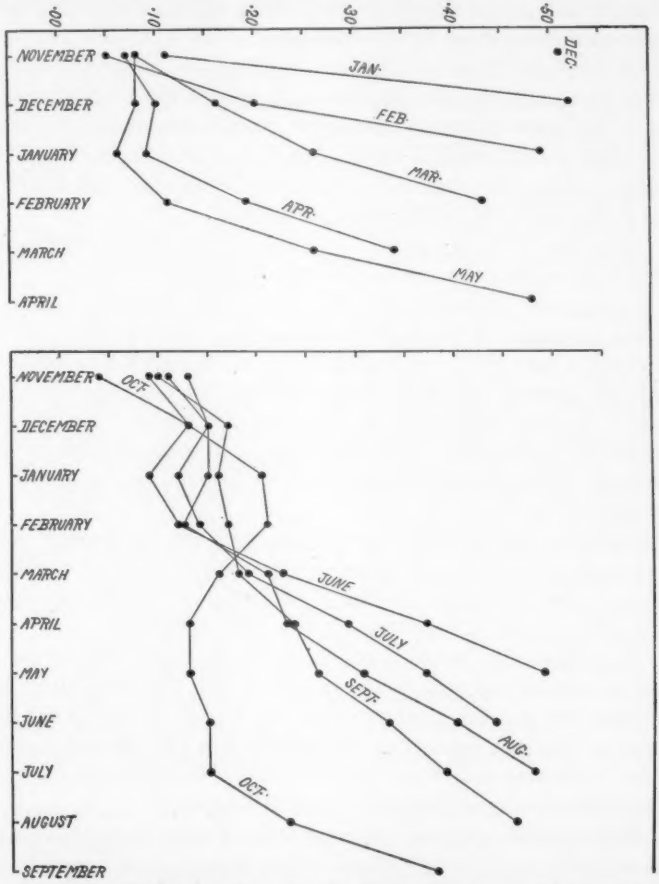

DIAGRAM 7.—Distribution of magnitudes of correlations between the records of individual months and the records of antecedent months of the same year.

between the homologous coefficients for the two years. We deduce from the ungrouped data in table 6

$$r = .9181 \pm .0130$$

This coefficient is very large indeed, and indicates a very close similarity between the coefficients measuring the relationship between the same combinations of months in the two years. It shows clearly that the correlations between the individual months do not differ in a merely haphazard manner but that there are definite and relatively rigid biological laws underlying these interrelationships.

When further data are available we shall have occasion to consider the relative magnitudes of the correlations between the correlations when birds of the same breed are compared at the same Station in different years, when the correlations for the same breed are compared at different Stations, and finally, when the correlations for different breeds are compared at the same Station or different Stations.

We now turn to a comparison of the magnitudes of the coefficients for the different combinations of months among themselves.

The reader will, of course, have noted that the mean value of the correlations is not large. It is only 0.244 for the series for 1916-1917, 0.196 for the series for 1915-1916, and 0.228 for the series for 1912 to 1919. The correlation between the series of correlations for the two years shows, however, that the coefficients for the different combinations of months differ among themselves. The significance of these differences in the magnitudes of the coefficients may best be brought out by graphic presentation.

The constants are divided into two series, the first (diagram 6) showing the relationship between the record of each month and that of each subsequent month, the second showing the correlation between the record of each month and that of each antecedent month (diagram 7).

On these diagrams, the verticals represent the subsequent or the antecedent months of the year as the case may be. The magnitude of the correlation between the production of any month (as indicated by the lettering on the lines connecting the dots for this month) and that of the months of the year is indicated on the scale of ordinates on the vertical for the antecedent or subsequent month in question.

In the preparation of these diagrams, it has seemed desirable to smooth out in so far as possible the probable errors of random sampling by using the averages of two independently determined constants. The values represented are the averages of the two series of correlations deduced from the 1915-1916 and the 1916-1917 series. The distribution of the several months between the two sections of the diagrams has been determined by clearness of presentation merely.

These diagrams show that in the Rhode Island Red as in the White Leghorn breed of poultry we may recognize the existence of two laws underlying the interrelationship between the productions of the individual months of the first year. These laws have been stated (HARRIS, BLAKESLEE and KIRKPATRICK 1918, p. 70–71) as follows:

"First, the correlation between the egg production of the individual months tends to become smaller as the months considered are more widely separated in time.

"Second, there is a more intimate correlation between the egg production of the autumn and winter months at the beginning and end of the contest year than between the egg production of these months and the productions of the spring and summer months."

Referring to the diagrams for details, we note from diagram 6 that for November, December, January and February production there is at first a rapid decline in the magnitude of the correlations with successively later subsequent months until a minimum value is reached for the production of the month under consideration and that of April or May. There is then an increase in the correlations for the production of these months and those of the months of June, July, August, September and October. The correlations for March are an exception to the other four months represented on this figure, in that correlation decreases as the successive months are more widely separated. This is also true for all of the months, April to August, represented on the second section of diagram 6.

Turning to the relationship between the egg production of individual months and that of preceding months, we note from diagram 7 that the correlations between January, February and March production and the production of preceding months decreases as the months become more widely separated in time. The correlations for April, May, June, July, August and September show a slight increase for the relationship between the production of these months and that of the earlier months of the year. The curve of the correlations of October production with that of the earlier months illustrates in a striking manner the existence of the two laws.

The comparison of the results for the Rhode Island Red breed with other breeds of poultry is reserved until the other constants, computed but not yet published, are available.

RECAPITULATION

This paper presents the results of a statistical analysis of the monthly egg records for the pullet year of 1658 Rhode Island Reds as recorded at the MASSACHUSETTS AGRICULTURAL EXPERIMENT STATION, Amherst, Massachusetts.

The following problems are considered:

1. The correlation between monthly record and annual production. The coefficients are shown to have a material positive value ranging from 0.325 to 0.634 in the 36 determinations made. The average values are $\bar{r}=0.5094$ for 1915-1916, $\bar{r}=0.5479$ for 1916-1917, and $\bar{r}=0.5363$ for 1912 to 1919.

These coefficients are of about the same order of magnitude as those already demonstrated for White Leghorn fowl (HARRIS and others, 1917, 1918). The regression of annual egg production on monthly egg production is, roughly speaking, linear. Prediction of annual egg production of groups of birds may therefore be made with relative ease from the records of an individual month by the use of equations of the type computed and shown to be effective for the White Leghorn breed (HARRIS, KIRKPATRICK and BLAKESLEE 1921; HARRIS, KIRKPATRICK, BLAKESLEE, WARNER and CARD 1921).

2. The correlation between monthly record and the total record of the other eleven months of the year. These values are, as might be expected, lower than those for the relationship between monthly production and annual production. They are, however, positive in sign and statistically significant throughout. They show, therefore, that the correlations between the records of the individual months and annual total is not due primarily to the inclusion of the record of the individual month under consideration in the annual total.

3. The correlation between the annual record and the deviation of the production of the individual months from their probable value. These coefficients show that the several months of the year differ greatly in their relative contribution to the annual egg record of unusual birds.

4. The correlation between the record of the individual months of the same year. All possible values of the correlation between the records of the individual months of the first year have been determined for two years individually and for the records for the entire period 1912 to 1919.

These coefficients are on the average small. The average value of the correlation is $\bar{r}=0.196$ for 1915-1916, $\bar{r}=0.244$ for 1916-1917, and $\bar{r}=0.228$ for the entire period, 1912 to 1919. The coefficients for the different permutations of months differ widely among themselves. This is shown by the fact that there is a correlation of .918 between the system of coefficients for 1915-1916, and that for 1916-1917. In their distribution the coefficients show the existence of two laws. First, the coefficient between the egg production of the individual months tends to become smaller as the months considered are more widely separated in time.

Second, there is a more intimate correlation between the egg production of the autumn and winter months at the beginning and end of the pullet year than between the egg production of these months and the productions of the spring and summer months. These two laws of the distribution of the magnitude of the correlations are to some extent mutually obscurant.

The foregoing conclusions are in general agreement with those already drawn for White Leghorns. Detailed comparisons between the more important commercial breeds will be made in a subsequent paper.

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STUDIES ON INHERITANCE IN PIGEONS. IV. CHECKS AND BARS AND OTHER MODIFICATIONS OF BLACK[1]

SARAH VAN HOOSEN JONES

Department of Genetics, University of Wisconsin, Madison, Wisconsin

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INTRODUCTION

A considerable interest has for some time been attached to the evolutionary, and in later years to the hereditary, relationships of the two color patterns in pigeons, known as blue black-barred (figure 5) and check (figure 3). This was due, in part at least, to the probable universality of these two patterns in many of the old domesticated races. According to BUFFON (1793), for instance, ALDROVANDUS about 1599 described the pigeon of Crete as having a bluish plumage, "and marked with two blackish spots on each wing." The same authority quotes WILLUGHBY (1678) as giving a similar description for the pigeon of Barbary. MOORE (1735) occasionally mentions "blue" types among the several varieties listed by him, as for example the Spot, the Jacobin and the Helmet. Both blue and checked examples are referred to in the "Taubenbuch" (ANONYMOUS 1790). Though the descriptions of these early writers are too brief to show with certainty that the "blue" to which they allude is

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similar to the blue with black wing bars, or blue with black check-marks of modern breeds, there is nothing to indicate a reference to any other color.

Writers of the early and middle nineteenth centuries, as BOITARD and CORBIE (1824) and EATON (1858), also mention blue and checked varieties of several breeds, describing them in detail. Later DARWIN (1868, vol. 1, p. 197) listed several breeds in which these two color patterns were known to occur.

Of equal if not even more importance than the mere presence of barred and checked types in established breeds was the occasional appearance of these two patterns, not only in presumably "pure" stocks of other colors, as black or white, but also in crosses of various colored birds not having, so far as was known, any barred or checked individuals in their ancestry. Descriptions of some such crosses made by the writers just cited, are presented by them in some detail. It will be sufficient to state here, however, that special attention was called to the unexpected cropping out of birds with one or the other of the patterns under discussion. As late as 1909 the French writer BAILLY-MAITRE refers to blue as the fundamental color and calls attention to its unexpected occurrence in various stocks.

At the same time the presence of the barred pattern among different species of pigeons in widely separated geographic areas was noted and described. DARWIN (1868, vol. 1, pp. 182–184) and TEGETMEIER (1868, pp. 26–27) describe these various species. The first one is *Columba leuconata*, which is blue with three wing bars and inhabits the Himalayas; those with two wing bars are *C. livia*, found on the coasts of Scotland and England, and *C. rupestris* of central Asia. Similar to these are *C. schimperi*[2] of Abyssinia and *C. gymnocyclus* of West Africa. These and others are detailed by SALVADORI (1893). More might be enumerated but the above will suffice to show the prevalence of the blue black-barred pattern among various species of the Columbidae.

Checked varieties for each of these wild species are not mentioned, but they may nevertheless exist. Such a variety of *C. livia* is well known and Darwin (1868, vol. 1, p. 184) mentions a checked specimen of *C. schimperi* in the BRITISH MUSEUM.

Somewhat similar checked patterns are found in *C. guinea* and many of the doves (mourning doves, ground doves, etc.); in fact a large number

[2] The writer examined a blue specimen of *C. schimperi* belonging to the FIELD COLUMBIAN MUSEUM of Chicago and was struck with its similarity to our common blue pigeons. This specimen was from Egypt.

of the individuals of the order Columbae exhibit checks. Whether the genetic behavior of the checks of *C. livia* and of the doves are similar is as yet a question.

From a study of the above-named species and many more DARWIN was led to the belief that *C. livia* was the progenitor of the domesticated pigeon, since it resembles the domesticated varieties in form more closely than do the other species. But of equal importance is the fact that it is easily domesticated and proves to be fertile with and to produce fertile hybrids by the domesticated pigeon.

Granting *C. livia* to be the progenitor of the domesticated races DARWIN easily accounted for the reappearance of checked and barred birds in supposedly pure stocks and in certain crosses, as reversions to the ancestral type. It is still generally conceded that *C. livia* is the progenitor of the domesticated varieties, and geneticists also interpret the unexpected appearance of checked and barred birds as reversions, but they attribute them to factor recombinations (COLE 1914, p. 343).

After conceding *C. livia* to be the ancestor of the modern races of pigeons, the next step was to determine the relationships of the two patterns, check and bar, and to discover if possible which was the original. It is this question which has produced a certain amount of speculation and some experimentation from the evolutionary and genetical standpoints.

DARWIN believed the barred type to be the original, while checked birds were probably due to "the extension of these black marks [black bars] to other parts of the plumage" (DARWIN 1868, vol. 1, p. 183). WHITMAN, on the other hand, assumed the opposite view, namely that the barred type resulted from a gradual clearing of the wings of checks "from before backwards" (WHITMAN 1919, vol. 1, p. 19), until the two-barred type resulted. He went further and stated that the evolution of these types was an orthogenetic one, basing his conclusions on certain results which he obtained from selection experiments.

The above are the two main evolutionary views, which obviously contradict each other. The other way of ascertaining the relations of the two patterns is by Mendelian breeding methods applied both to domesticated varieties and to birds of the wild stock representing the two patterns. These genetic relationships have been fairly well established by STAPLES-BROWNE (1908, 1912) and BONHOTE and SMALLEY (1911), who advanced data showing the independent Mendelian inheritance of the two patterns.

In view of the foregoing, the object of this paper is to show the heredi-

tary relationships of the two types under consideration to the other colors in pigeons, with special reference to black; secondly, to show from a microscopic study of pigment arrangements and breeding experiments the interaction of several factors affecting blue and black; and lastly to interpret WHITMAN'S results on a genetic basis.

The data which follow are taken not only from special matings made by the writer at the WISCONSIN AGRICULTURAL EXPERIMENT STATION during a period of three years, but also from the entire set of pigeon records dating back to the beginning of the work by Professor COLE at the RHODE ISLAND STATION in 1907. As a consequence many of the matings used by him in his 1914 paper and also in the 1919 paper by COLE and KELLEY are repeated here.

THE "BLUING" SERIES

There is a wide range in the amount of blue which may occur, from full black, where no blue at all is present, to a type known as barless, in which nearly the whole bird is blue. The variations form a series of gradations of increasing "bluing." The six types which have been distinguished in this work are fairly distinct, though there is some intergrading in certain cases. The breeding behavior, however, seems to indicate their genetic distinctness. It is probable that the intergrading is due, in some cases at least, to modifying factors of one sort and another; and it is also not improbable that other genetically distinct grades may exist besides those described. These six types are described in the order of their progressive bluing (decreasing amount of black in relation to blue), and it is interesting that they appear to be epistatic in their hereditary manifestation in the same order, i.e., each to the one that follows. It is to be noted that blue appears in the rump and in the outer vanes of the outer tail feathers independently of this series.

"Full black" (figure 1) as used in the present paper refers merely to the absence of blue everywhere except in the rump and outer vanes of the outer tail feathers. Blue appears first in the tail, making the "black blue-tail," and its further invasion results in the "checked," "sooty," "blue black-barred" and "barless" types, all of which, however, have the characteristic blue tail. Full black takes no cognizance of kitiness (reddish), often present in the flights of black pigeons, nor of white spotting, nor, as mentioned above, of a dark blue rump or light outer vanes of outer tail feathers. A bird might possess all these characteristics, but so long as it lacked the blue tail with black terminal band it would be classified as a full black.

"Black blue-tail" is the next stage below full black. The chief distinguishing characteristic from black is the blue tail with a black terminal band. This pattern shows variability in itself, since all birds entirely black except for blue tails (figure 2) to those with blue or almost white rumps and with or without some bluing in the primaries, but with unchecked wing coverts are included in this class.

FIGURE 1.—Full black with uniform rump (grade 5) and uniform outer vanes of outer tail feathers. (Wisconsin No. 1673A.)

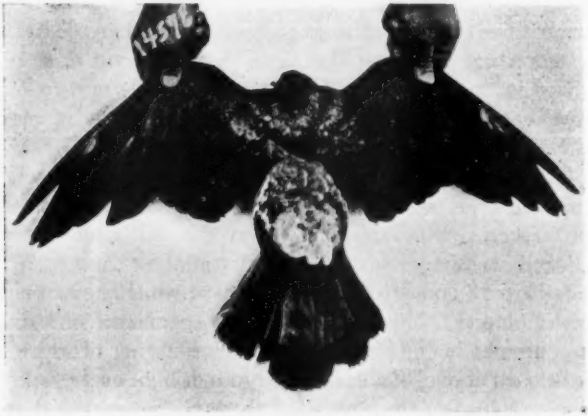

FIGURE 2.—Black blue-tail with uniform blue rump (grade 3) and light outer vanes of outer tail feathers. The white feathers in the rump are not considered. (Wisconsin No. 1457E.)

References to this type are not very numerous. DARWIN (1868, vol. 1, p. 184) in describing the Rock Pigeon of Madeira says, ". . . others are chequered, like *C. affinis* from the cliffs of England, but generally to a greater degree, being almost black over the whole back; . . . . ." The "reversionary blues" described by STAPLES-BROWNE (1908, 1912) belong in this class.

"Check" originates from the so-called checked appearance of the wing (figure 3). This condition is caused by the presence of two black marks situated respectively in the inner and outer vanes of the wing coverts, the central and proximal portions of which are blue. The rest of the plumage of checked birds is blue with the invariable exception of a

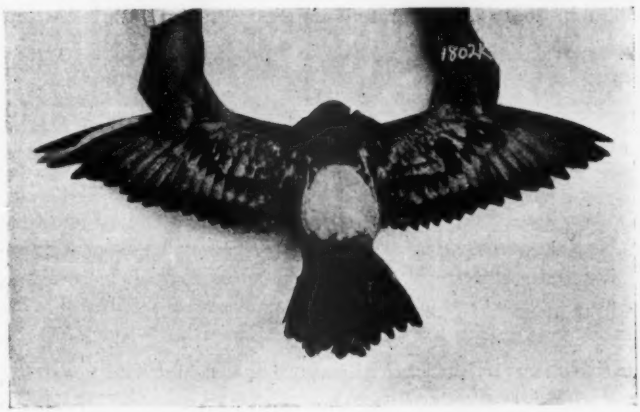

FIGURE 3.—Medium check with extreme light blue rump (grade 1); outer vanes of outer tail feathers only slightly lighter than those of the other tail feathers. (Wisconsin No. 1802K.)

black terminal band on the tail and of the not infrequent presence of checks on the upper back. The rump may be either very light, almost white, or a shade of blue uniform with that of the wing coverts, or any shade between these two colors.

"Sooty" is the fourth variation of the bluing series to be considered. The black blue-tail represents a character which is blacker than the check, while the sooty character is representative of the opposite condition. Sooty, as the name implies, comprises those individuals whose wing coverts have a mere sprinkling of black, giving the bird a sootied appearance (figure 4). The black on the wing coverts is so small in

amount that it fails to take on a definite pattern as it does in the typical check.

It is not at all difficult to differentiate between sooty and check, as the sprinkling of black on the wing coverts is easily distinguished from the definite black spot of the check mark.

References to this type are also few. CHAPMAN (1911, p. 5) mentions sooty blues. STAPLES-BROWNE (1912) in describing the offspring from the Rock-Fantail cross says that the classification of birds into "chequered" and "non-chequered" groups was complicated by several individuals which he termed "intermediates" and described "as showing a slight darkening of some of the lower wing coverts, which is not noticeable unless the bird is caught." This description is in keeping with what is referred to as sooty in the present paper. Although WHITMAN does not

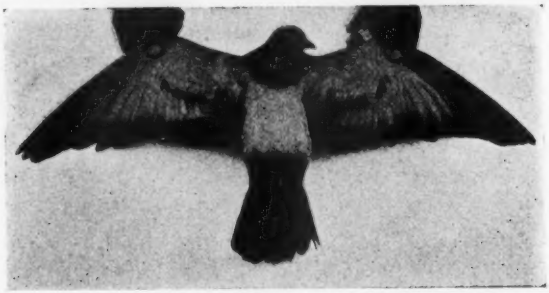

FIGURE 4.—Sooty blue with light blue rump (grade 2) and light outer vanes of outer tail feathers. (Wisconsin No. 1777A.)

definitely discuss this character, the plate of *C. oenas* (WHITMAN 1919, vol. 1, plate 9) appears to depict the character very well.

"Bar" refers to the pattern commonly called "blue black-barred." The wings of a barred bird are blue with two transverse black wing bars, one of which extends through the tertiaries and innermost secondaries, while the second extends through most of the secondary coverts (figure 5). The so-called blue of the pigeon is in reality a gray which, according to COLE (1914), corresponds to RIDGWAY'S "gull gray." The tail and rump are similar to those of the check, but the back is free from any check marks.

"Barless," the sixth and last variation, is, so far as known at present, the lowest stage in the bluing series. As the name implies, the wings lack any bars, which makes the distinction between this type and bar very

easy. In the barless individual the so-called blue has entirely replaced the black wing bars leaving a clear blue wing, except for the darkened tips of the primaries, secondaries and tertiaries.

This character has been known for some time. DARWIN (1868) mentions as barless a sub-variety of the Swallow, of German origin, pictured by NEUMEISTER. LYELL (1887) calls attention to the same pattern in the Ice Pigeon and a variety of the Swiss Pigeon. SCHACHTZABEL (1906) pictures several barless varieties as follows, the Strasser, Goldgimpel, (which has a yellow body and blue barless wings), the Pfaffen and Eichbuhlertaube. BAILLY-MAITRE (1909) also names a barless variety of German origin, "Feld-Tauben." Both the barless Strasser and Ice Pigeon as well as barless varieties of the Swallow and Homer are produced in this country. Figure 6 represents the latter breed.

FIGURE 5.—Blue black-barred with light blue rump (grade 2). (Wisconsin No. 1790A.)

Genetic relationships of black, check and bar

The phenotypic differences between these three characters depend upon the presence of varying amounts of the two so-called colors, black and blue, the check being the intermediate type. A further difference between the two colors is one of pigment-granule arrangement. COLE (1914) showed these granules in the barbules of a black feather to be evenly distributed and those in a blue feather to be clumped. These two conditions have been found, as might be expected if checks are a combination of black and blue, existing side by side in the feathers of checked birds. It is this difference in pigment arrangement that produces the two different optical effects.

COLE also showed that full black is dominant to the barred type. In view of the microscopic study just discussed he postulated a factor *S* which referred to the spreading of the pigment granules evenly throughout the barbules of black feathers, while *s* indicated the clumped condition in blue ones. Table 1 is presented as furnishing further data on the dominance of black birds known to be *SS* to bar (*ss*). From three such

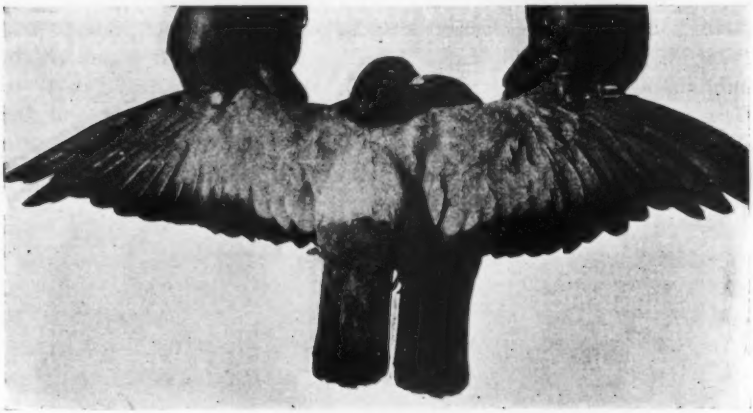

FIGURE 6.—Blue barless Homer with light blue rump (grade 2). (Wisconsin No. 1751A.)

matings 22 full-black offspring resulted. COLE'S data and those of the writer regarding the segregation of the *S* factor will be presented and discussed later. It may be stated here, however, that black differs from bar by a single factor.

TABLE 1

Black (SS) by bar (ss).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED *S*-BLACK	EXPECTED *S*-BLACK
1033	999A	*sscc*	7A	*SS(CC)**	10	10
1746	1671A	*SS(CC)*	1470F	*sscc*	7	7
1803	1462H	*SS(CC)*	1670A	*sscc*	5	5
Total (3 matings)					22	22

* Letters inclosed in parentheses indicate uncertainty as to this portion of the formula.

The next step was to establish the relation of black to check. Since the black birds in the colony at the WISCONSIN STATION were known to

be heterozygous for various color characters including those for check and bar, the purchase was made of several black Tumblers, presumably "pure" for black, that is, not having any barred or checked ancestry. The checked parents were from colony stock and were known to be heterozygous. The breeding results proved the blacks purchased to be homozygous, and it is obvious that black is dominant to check, since in six matings 57 full-black birds were obtained, and as many as 22 in a single mating (1686).[3]

When two blacks homozygous for *S*, or when at least one parent is of this composition, are mated together, only full blacks result. Six such matings gave a total of 61 full-black offspring.

That there is apparently a single-factor difference between black and check is shown by the very close 3 : 1 ratio obtained in table 2. Five matings of full-blacks to full-blacks when both were known to be heterozygous give a total of 25 blacks to 8 checks, the expected being 24.75 to 8.25.

TABLE 2

Segregation of S and s in presence of CC.*

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED		EXPECTED	
					S Black	*C* Check	*S* Black	*C* Check
554+	450X	*SsC(C)*	450Y	*SsC(C)*	6	1	5.25	1.75
662+	493B	*SsC(C)*	454B	*SsC(C)*	8	1	6.75	2.25
1015+	790B	*SsC(C)*	799A	*SsC(C)*	4	1	3.75	1.25
1025+	862A	*SsC(C)*	$862B_3$	*SsC(C)*	3	3	4.50	1.50
1812	1685C	*SsC(C)*	$1594Q_3$	*SsC(c)*	4	2	4.50	1.50
Total	(5 matings)				25	8	24.75	8.25

* Only those matings from which 5 or more offspring resulted, and only those for which complete descriptions were made, have been used in the compilation of this table.

Having shown black dominant to both check and bar and differing from each by a single factor, the relation of check to bar will next be discussed. BONHOTE and SMALLEY (1911) state that they have accurate records on fifty-seven matings of check by check, from which 229 checked offspring resulted. Reference to the work of STAPLES-BROWNE (1912) gives one mating of check by check producing ten offspring which,

[3] Many of the tables giving detailed results of individual matings have been omitted from this paper in order to economize in the cost of printing. They will be found in full in the original thesis deposited in the Library of the UNIVERSITY OF WISCONSIN.

according to the author, indicates that at least one parent was homozygous for check. He also presents a mating of check by bar giving eight checked squabs, indicating the dominance of check to bar. Similar data are available from WHITMAN (1919, vol. 2, table 72, p. 104). Two checked wild Rocks produced 16 checked offspring and no barred, showing without doubt that one parent at least was homozygous for check. In the present experiments a mating (1607) of homozygous check by bar gave 8 checked offspring and two others (1596, 1743) of a black blue-tail male, known to be homozygous for *C*, with barred females produced 12 check and 2 black blue-tailed progeny. This male must have been heterozygous for black blue-tail. These and the earlier results demonstrate that checks (or black blue-tails) homozygous for *C*, when mated to checks or bars, do not throw individuals lower in the series than checks.

Data on the segregation of the factor for check are also numerous. STAPLES-BROWNE gives three matings of check by check in which both parents are heterozygous. The result of these matings was 21 check to 12 bar, which is not very close to a 3:1 ratio. BONHOTE and SMALLEY (1911) give two similar matings from which 13 checked and 4 barred offspring were obtained, which numbers are very close to the above ratio. The work of NUTTAL (1918) might offer some available material on this point if the matings had not been complicated with the known sex-linked *A*-factor which restricts black, and possibly with others. WHITMAN (1919, vol. 2, table 72, p. 104) obtained from two matings of checked birds, presumably heterozygous judging from the patterns of the progeny, 23 checked offspring and 5 barred. One of the parents of one mating was procured from a fancier and the other parent was a stray pigeon, while the parents of the second mating were both original wild Rocks from the Cromarty caves of Scotland. These figures also, considering the numbers, fit a 3:1 ratio fairly closely. Eleven matings made by the writer, in which checked birds heterozygous for this factor were interbred, gave 59 checked (excluding 1 possible black blue-tail) to 18 barred offspring. This is very close to a 3:1 ratio (57.75 : 19.25). A summation of the foregoing results gives 116 checked to 39 barred birds, where the expectation is 116.25 to 38.75, seeming to demonstrate that check and bar differ by a single Mendelian factor.

Further data, from matings in which 1:1 ratios are expected, are available from STAPLES-BROWNE and WHITMAN. The latter presents two such matings giving 9 checks to 10 bars, and the former (STAPLES-BROWNE 1912) two matings which give 5 checked to 18 barred offspring. The results of the last two matings are certainly not very close to expec-

tation. A tabulation of twenty-one matings of heterozygous checks mated to bars, exhibits a fair 1:1 ratio (87:105).[4] $\frac{\text{Deviation}}{\text{Probable error}}\left(\frac{.09}{.05}\right)=1.80$ indicates that the discrepancy may be due to random sampling.

Blacks, then, throw blacks, checks, and, as will be shown presently, also bars, while checks throw only checks and bars. Bars, however, produce neither blacks nor checks but bars only, as is shown by the following results obtained from many matings in several stocks of bars to bars. BONHOTE and SMALLEY (1911) secured from twelve such matings 41 barred offspring, STAPLES-BROWNE (1912), 198 barred birds, and WHITMAN (1919), 16 barred individuals from six matings of barred wild Rocks. The writer's data show that forty-nine barred offspring resulted from six matings of bar to bar and one mating of bar to barless (1770). Three hundred and four barred birds have, accordingly, been obtained from at least four entirely different stocks constituting 53 different matings of bars to bars, which shows fairly conclusively that barred birds breed true.

In order to explain the foregoing results a factor *C* for check has been postulated. It is not linked with *S* but can act only in the presence of *s* to produce the checked pattern. In other words *S* is epistatic to *C*. When neither *S* nor *C* are present the barred type is the result. Blacks, then, may or may not carry *C* and can consequently be of the following compositions, *SSCC*, *SSCc*, *SScc*, *SsCC*, *SsCc*, *Sscc*. Checks, on the other hand, can be of but two sorts, *ssCC*, *ssCc*, while the barred type can be only *sscc*.

In order to further illustrate such a hypothesis the data in tables 3 and 4 are presented. Table 3 shows four matings of blacks by blacks heterozygous for *S* and *C*, in which case a 12:3:1 ratio is expected. The total for each of the three classes for which complete descriptions are given is small (15:6:4). As a consequence the closeness of fit (P) is poor (.086). When, however, all individuals are included the ratio becomes 25:6:4 and the value for P is then .461 which is a fair fit. The matings of table 4 consist of black birds heterozygous for *S* and *C*, mated to bars, which give an expected ratio of 2:1:1. The check class is low and the bar class high. Consequently the value for P (.154) can hardly be called fair. It is reasonable to suppose that the low values for P are due to the small numbers from which they are calculated and not to a misinterpretation of the data.

[4] The 105 bars include 4 sooty birds, which can be legitimately included in the present instance, however, as "non-checks."

TABLE 3

Blacks (SsCc) by blacks (SsCc).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED			EXPECTED			NOTES
					S Black	*C* Check	*Ba* Bar	*S* Black	*C* Check	*Ba* Bar	
1296	1033A	*SsCc*	1033B	*SsCc*	4	2	2	6.0	1.5	.5	2 blacks not included, poor descriptions
1305	1033D	*SsCc*	1033E	*SsCc*	7	2	1	7.56	1.89	.63	3 blacks not included, poor descriptions
1110+ and 1332	905B	*SsCc*	864A	*SsCc*	2	1	1	3.00	.75	.25	4 blacks not included, poor descriptions
1126+ and 1311	962A	*SsCc*	915B	*SsCc*	2	1		2.28	.57	.19	1 black not included, poor description
Total (4 matings)					15	6	4	18.72	4.68	1.56	χ^2=4.924 P=.086
Total all birds included					25	6	4	26.28	6.57	2.19	χ^2=1.609 P=.461

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TABLE 4

Black (SsCc) by bar (sscc).

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	OBSERVED			EXPECTED			NOTES
					S Black	*C* Check	B_a Bar	*S* Black	*C* Check	B_a Bar	
1448	1341D	*sscc*	915B	*SsCc*	8		4	6.00	3.00	3.00	2 not used
1454	1385B	*SsCc*	1242A	*sscc*	6		4	5.00	2.50	2.50	1 not used
1484	962A	*SsCc*	1432A	*sscc*	1	2	2	2.50	1.25	1.25	
1681	1512R	*SsCc*	1657Z	*sscc*	1	1	2	2.00	1.00	1.00	1 not used
1682	1448T	*SsCc*	1668A	*sscc*	4	5	4	6.50	3.25	3.25	
1742	1666G	*sscc*	1454V	*SsCc*		1	2	1.50	0.75	0.75	
1748	1657J	*sscc*	$1616A_2$	*SsCc*	5	1	1	3.50	1.75	1.75	
1767	1532D	*sscc*	1699Q	*SsCc*	7	3	5	7.50	3.75	3.75	
1824	1659S	*sscc*	1605V	*SsCc*	2	1	1	2.00	1.00	1.00	
1859	$1553J_2$	*SsCc*	1657Z	*sscc*		1	1	1.00	0.50	0.50	
Total (10 matings)					34	15	26	37.50	18.75	18.75	

$\chi^2 = 3.782$ $P = .154$.

The description of the inheritance of these three patterns corresponds somewhat to that offered by COLE (1914) for the occurrence of STAPLES-BROWNE's "reversionary blues." COLE suggested a factor *T* which, like the *C* factor, acted only in the absence of *S*. He also pointed out that the blues which STAPLES-BROWNE recovered from his second generation of black Barb and white Fantail cross were not the same as those to which DARWIN referred. These birds instead of having clear blue wings with two black wing bars as described by DARWIN and referred to in this paper as the barred type, had black wings with indistinct blacker bars and blue tails with black terminal bands. In offering such an explanation for STAPLES-BROWNE's data, COLE differentiated between typical full blacks and blacks with blue tails, as the writer has done for blacks and checks, but in presenting his own data on the segregation of the *S* factor all black blue-tailed birds and also checks were included in one class with the full-blacks, while the typical blue black-barred birds were put in the other class. Data have been presented to show that blacks and checks differ by the *S* factor and more data will be given later to show that black blue-tailed birds do not carry *S*. Consequently the *S* factor as presented here differs from that postulated by COLE for his own data, but corresponds to that offered by him in explanation of STAPLES-BROWNE's findings. According to the present interpretation it refers only to full-blacks, while all black blue-tailed and checked birds are the result of its allelomorph (*s*) plus two other factors, *T* and *C*. On such a hypothesis COLE's data showing the segregation of *S* should better fit a 15:1 ratio than a 3:1. While his numbers (19:3) based on the offspring from three matings are too small to prove this point one way or the other, they at least fit a 15:1 ratio quite as well as a 3:1.

The epistatic series, black, black blue-tail, check, sooty, bar and barless

The relation of black to check and bar has been discussed. It is now proposed to consider the other members of the series.

Data giving the complete Mendelian inheritance of black blue-tail are insufficient. What there are, merely show that it appears to behave toward black very much as does check. Seven matings of blacks to blacks which throw black blue-tail, gave 21 of the former to 9 of the latter. It may be assumed that these blacks were heterozygous for *S* and homozygous for *T*, the factor determining black blue-tail, since they produced no offspring lower in the series. This result is suggestive of a single-factor difference.

Various matings of black blue-tail to other types in the series are given in sections A, B, C and D of table 5. In the later sections are various combinations of other types lower in the series. The numbers in most cases are too small to have much significance as to ratios, but it is to be noticed that in general the results confirm the conclusion that in any mating offspring are not produced higher in the series than the high parent. The one or two exceptions will be discussed below. In many of the matings there were offspring which died too young for description, or which were for other reasons insufficiently described; these might have changed the ratios materially.

Section A consists of two matings of blacks by black blue-tails. Three types are produced, blacks, black blue-tails and checks. In section B there is an exception to the rule that the grade of the offspring is not higher than that of the parents, for a pair of black blue-tail birds have produced three full-black offspring. By hypothesis black blue-tails do

TABLE 5

Matings of blacks, black blue-tails, checks, sooties and bars.

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	*S* BLACK	*T* BLACK BLUE-TAIL	*C* CHECK	S_0 SOOTY	B_B BAR
A. Black by black blue-tail									
168+	28B	*SsTtC(C)*	71A	*ssTtC(C)*	3	1	6		
1076+	841A	*ssTtC(C)*	799B	*SsT(T)*	1	1			
B. Black blue-tail by black blue-tail									
1592	1457E	*ssTtC(C)*	1457N	*ssTtC(C)*	(3)	2	2		
C. Black blue-tail by check									
808+	194B	*ssTtC(C)*	559A	*sstC(C)*			4		
1610	1457Q	*ssTtC(C)*	837B	*sstC(C)*			2		
1694	1533V	*ssTtCc*	1607W	*sstCc*			3		1
D. Black blue-tail by bar									
1596	1533K	*ssTtCC*	1448E	*sstcc*			6		
1608	1533V	*ssTtCc*	1472Q	*sstcc*			12		
1743	1533K	*ssTtCC*	1443C_2	*sstcc*		2	12		
1744	1533V	*ssTtCc*	1454M	*sstcc*		1	3		
E. Black by bar throwing sooty									
1472	829B	*Ss(TT)* *Cc*S_0S_0	1296N	*sstccs*$_0$*s*$_0$	5		1	3	2

MATING	♂♂	COMPOSITION	♀♀	COMPOSITION	*S* BLACK	*T* BLACK BLUE-TAIL	*C* CHECK	S_0 SOOTY	B_0 BAR
			F. Check by bar throwing sooty						
30+	26A	*ssttccs$_0$s$_0$*	27A	*sstt*C*cS$_0$s$_0$*			6	1	8
1453	1077A	*ssttccs$_0$s$_0$*	1196A	*sstt*C*cS$_0$S$_0$*				1	2
1652	1526H	*sstt*C*cS$_0$s$_0$*	1443C[2]	*ssttccs$_0$s$_0$*			4	2	1
1802	1704E	*sstt*C*cS$_0$s$_0$*	1788A	*ssttccs$_0$s$_0$*			3	1	2
Total (4 matings)							13	5	13
Expected (2:1:1 ratio)							15.5	7.75	7.75
			G. Check by sooty						
1342	1091J	*ssCc*(S_0)	1173A	*sscc*(S_0)				1	
1765	1708B	*sscc*(S_0)	1607B$_2$	*ssCc*(S_0)			6	5	1
1760	1657T	*ssCc*(S_0)	1652B	*ssccS_0s$_0$*			1	1	1
1759	1638D$_2$	*ssC*(*C*S_0)	1173A	*sscc*(S_0)			1		
			H. Sooty by sooty						
1482	1385A	*ssccS_0s$_0$*	1173A	*ssccS_0s$_0$*				2	2
			I. Sooty by bar						
1664	1462H	*ssttccs$_0$s$_0$*	1491D	*sstt*C*cS_0s$_0$*				3	4
1798	1777A	*sstt*C*cS_0s$_0$*	1665B	*ssttccs$_0$s$_0$*				1	2
1669	1568U	*sstt*C*cs$_0$s$_0$*	1668A	*ssttccs$_0$s$_0$*				1	4
Total (3 matings)								5	10

not carry *S* and hence should not produce blacks. It so happens, however, that the preponderance of the data presented in substantiation of the theory on the genetic relations of the various blue types to black are taken from matings of Homers and Tumblers, while these three exceptions occurred in a single mating of a pair of Fantails. It seems possible, therefore, that this breed may carry some modifying factors which disturb the usual relations.

Such a presumption is further substantiated when the several matings of black blue-tailed Tumblers and Homers to checks and bars of the same breeds (sections C and D) are considered. In seven such matings 46 offspring were produced and none was full black. Full-black, then, may carry the factor for black blue-tail (*T*), but black blue-tails, when bred to bars or checks, do not (with the exception above) throw full-blacks, that is, they do not produce offspring with more black than they themselves show.

The typical check is the next stage lower in the series. The distinction between check and black blue-tail is not as readily made as between

full-black and black blue-tail. It is often difficult to differentiate between a very slight check (figure 11C) and a black blue-tail, as some birds have only a very little checking in a few of the greater wing coverts. In this case the classification has to be arbitrary, and for present purposes those birds with any checking on the wing coverts are considered as checks.

The breeding behavior of check, as already intimated, is similar to that of black blue-tail. In eleven matings of typical checks to checks (see page 476) only checks were produced, with one doubtful exception in which two slight checks produced a black blue-tail.[5] The squab died young, however, and at this time showed two shades of black instead of black and blue. Had it lived to maturity it might have moulted to a typical check, the poor black becoming at least somewhat blued. In the twenty-one matings of checks to bars (page 477) no offspring with more black than that shown by the checked parents resulted.

The writer's data on the Mendelian behavior of the sooty character are meager, as they were for the black blue-tail pattern. Nevertheless, they illustrate the same point. Sections E and F of table 5 show that full-blacks and checks when bred to blues may throw sooties. The numbers obtained in section F are, so far as they go, in fair accord with the present hypothesis. The checked parents are *Cc* and carry the factor for sooty in a heterozygous condition ($CcS^{o}s_{o}$), for they throw sooties when bred to bars which lack both check and sooty ($ccs_{o}s_{o}$). In this case a 2:1:1 ratio is expected. There is a preponderance of blues, which, however, may be due to the fact that the early descriptions made for the birds of mating 30+ were not as detailed as were the later ones for the other matings, and consequently, some of the 8 barred birds might be sooties. Section G gives the results of breeding sooties to checks, in which case sooties and checks are recovered. When sooty is bred to sooty or to bar (sections H and I) only sooties and bars result, no checks or forms higher in the series than the sooty being obtained. A 1:1 ratio is expected from the matings given in section I. There is a decided preponderance of blues, which is attributed to small numbers.

Bar, the fifth in the present series, has already been discussed in detail. It is easily differentiated from sooty and check by a complete absence of any black on the wings except the black bars. This type, it may be remembered, bred true; it did not produce offspring with more black than shown by the two wing bars.

[5] It is possible that the arbitrary point of demarkation referred to in the preceding paragraph may be genetically wrong and that these *slight* checks are really black blue-tails.

All that can be said at this time regarding the inheritance of barless is that it is apparently recessive to bar. A barred Homer crossed on a barless Homer gave four barred offspring and one which died before the wing bars developed, that is, before they normally develop in pure barred stock. In another mating the male was black but known to be heterozygous for *S* and to carry the factor for barring. The female was a barless Swallow. Only three offspring resulted, of which two were blue with black bars and one was a full-black with blacker bars. The data, though very few, nevertheless indicate that barlessness (b_a) is recessive to bars (B_a). No F_2 data have as yet been obtained, but there is every reason to believe that either complete segregation or at least a series which will show no more black than the blue black-barred grandparent, will result.

As has been frequently pointed out the blacker types throw individuals of various lower but not of higher grades. For instance, blacks may throw blacks, black blue-tails, checks, sooties and bars; black blue-tails (with one exception) throw black blue-tails, checks, sooties and bars; and so on, down the series.

Apparently, then, these six characters form an epistatic series illustrated in figure 7. This relation of several factors might naturally suggest multiple allelomorphs. They do not, however, fall into this category, since blacks known to be heterozygous for bar, when bred to bars, have produce checks (table 4, page 479), which is inconsistent with the theory of multiple allelomorphs. Furthermore, if these factors formed a multiple-allelomorph series no more than 3 types could ever be recovered from any one cross. On the epistatic-series interpretation it should undoubtedly be possible, however, to obtain the six types of the present series from suitable crosses, and 4 have actually resulted (table 5, section E) in a cross of a black by a bar.

So far as the data go the various factors are apparently not linked, but each is carried on a separate pair of chromosomes. Furthermore, these several factors do not have a cumulative effect as in quantitative inheritance, but each is capable of producing its particular effect in the absence of the ones higher in the series.

This series pertains to the orderly relation of various conditions of one character, these conditions being due to factors not allelomorphic to any of the other factors. Obviously, such an epistatic series cannot, as BREITENBECHER (1921, p. 66) suggests in his paper on multiple allelomorphs in Bruchus, also form a multiple-allelomorph series.

The epistatic series is of special interest in the light of WHITMAN'S selection experiments. He was able to select for fewer and fewer checks

until he obtained a typical blue black-barred wing and finally one even without bars, but he was unable to reverse the process. These results led him to believe that the check pattern had probably evolved in an

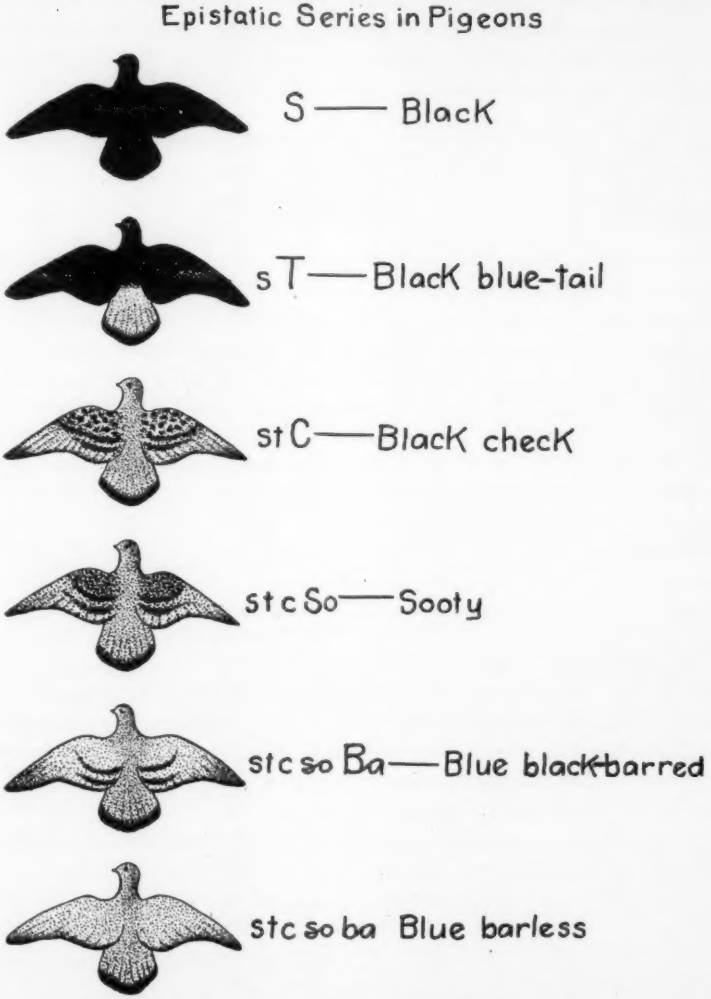

FIGURE 7.—Six distinguishable grades of the epistatic series showing the successive decrease in the amount of black (spread pigment) in relation to blue (clumped pigment).

orthogenetic fashion and that this type of evolution was continuing. His results, however, are quite in keeping with the genetic behavior of the factors in the epistatic series just discussed. Obviously mere heterozygosis is sufficient for obtaining the lower grades of check and bar, while it is very apparent that the higher grades can only result from dominant mutations. This would account for WHITMAN's failure to obtain offspring with much checking from parents with only a little.

If the wild Rock is the progenitor of the domestic races of pigeons it seems evident, then, that black and black blue-tail have occurred by dominant mutations.

Relation of the factors, S, T, C, and S_s, to other known heritable colors

COLE (1914) showed that the *S* factor could be carried by red and yellow individuals. In other words the presence of *B*, the factor producing black pigment,[6] was necessary for the manifestation of *S*. In a similar way the presence of *B* is necessary for *C* to act, but *S* as already pointed out, must be absent. The same is true of the *T* and S_s factors. Seven matings in which reds were mated to bars produced blacks, checks, sooties and bars, obviously showing that these reds carried *S*, *C* and S_s. If more birds had been tested, no doubt some carrying *T* would have been found. Nine matings of yellow and bar proved that yellows also transmit these four factors.

The *C* factor is carried in a similar way by whites, as shown by various crosses made by STAPLES-BROWNE (1912) of bars on whites with the result that the offspring were frequently checked. There is no reason to suppose that others with *S*, *T* and S_s do not also exist.

The six patterns discussed are distinguishable in the dilute series as in the intense. That is, parallel to the first five grades of the intense series there are full-duns, dun silver-tails, dun checks, sootied silvers and silvers with dun wing bars. By analogy there should also be silver barless. Difficulty was sometimes found, however, in differentiating these dilute types because of the variations in the shades of dun. Many full-duns, that is, *S* birds, may have darker terminal bands on their tails, which complicates the usual easy distinction between *S*, *T* and *C* birds in the intense series, since the tails of the latter are as a rule uniformly black without a blacker terminal band.[7] In questionable cases of the dilute

[6] The action of *B* may perhaps better be considered as *extending* black pigment, making it analogous to *E* in mammals (see COLE and KELLEY 1919, footnote 4, p. 186).

[7] Two individuals of the *SI* type have been noted among the 1920 offspring, as having a darker terminal band with a lighter area just posterior to it. This area has somewhat of a bluish cast. When examined microscopically, however, it shows only clumped pigment as does the corresponding area in duns (*Si*).

series a microscopic study of that part of the tail anterior to the band, where clumped pigment is expected in checked and barred birds, was often necessary.

The next consideration was to correlate, if possible, the grades of the epistatic series with the various shades of red and yellow produced by the sex-linked black-restricting *A* factor. This, however, proved impossible with the present knowledge of the many variations of color due to this factor. There exist the so-called red-barred and red-checked types, but it was sometimes found upon testing that these did not always correspond to what was meant by check and bar in the *a* series. It is plain that the only way to determine the corresponding patterns in the two series is to test the many varieties of the *A* series by breeding to *a* bars. Until such work has been done an attempt to distinguish the *A* epistatic series will be postponed. Preliminary experiments demonstrated that *A*-factor birds may carry S, C and S_e. If more individuals had been tested, some carrying *T* would no doubt have been isolated as well.

While, then, the factors which produce the various grades of the *a* epistatic series can act only in the presence of *B* and absence of *S*, they can be carried by *b* and *S* individuals, by whites and by restricted reds. In other words they may be present in any of the eight known heritable colors of pigeons, but can not show except under certain favorable factorial conditions.

UNIFORM AND LIGHT OUTER VANES OF OUTER TAIL FEATHERS

The variation in the color of the outer vanes of outer tail feathers represents another modification of blue and black. Anyone familiar with pigeons is acquainted with the so-called light outer-vane condition found in both blue- and black-tailed birds (figures 12 and 2). It is restricted to that part of the outer vanes of the outer tail feathers proximal to the region occupied by the black terminal band characteristic of blue-tailed birds. This entire region or only the outer edge may be affected. DARWIN and LYELL call attention to it in descriptions of various breeds of pigeons, especially the wild Rock. The contrasting condition, uniformity, refers to the fact that this portion of the outer vane is similar in color to the other tail feathers, that is, in *S* or black-tailed birds it is black (figures 1 and 8A) while in blue-tailed or *s* birds it is blue (figures 9 and 8C).

A microscopic examination of the two conditions, uniform outer vane and light outer vane, in *S* birds (full-black, with black tails) shows them to be different. The pigment in the former (figure 8A) is spread, while in the latter (figure 8B) it is clumped. The uniform outer vanes of blue-

tailed individuals (figure 8C), however, show clumped pigment. This is to be expected, since the factor *s* has already clumped the pigment and, as mentioned above, uniformity merely means that the outer vanes shall

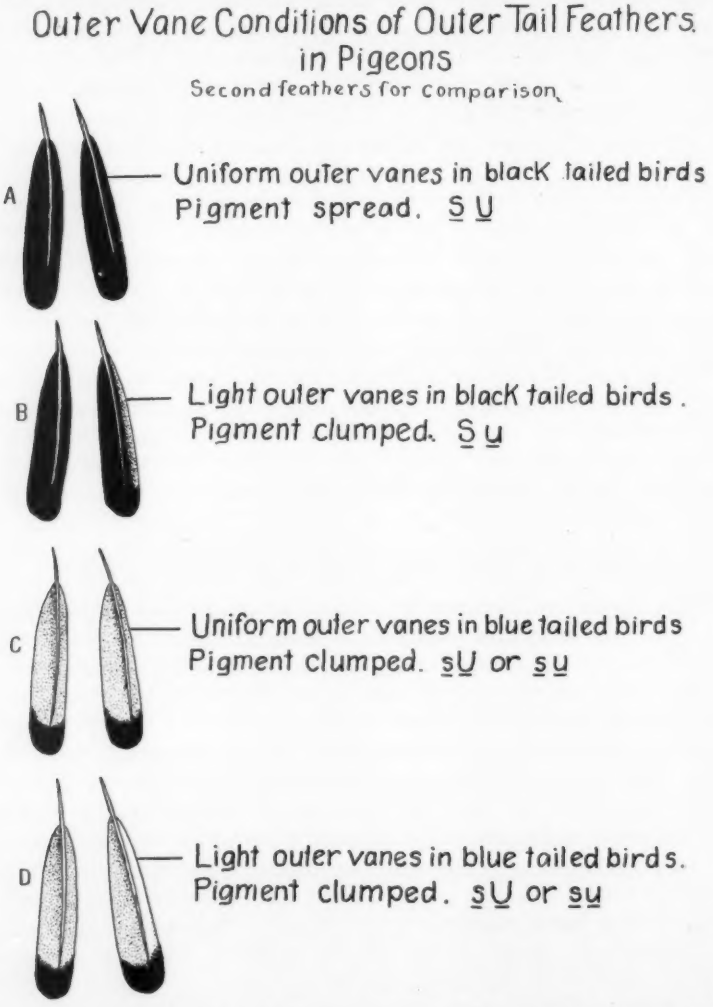
Outer Vane Conditions of Outer Tail Feathers in Pigeons
Second feathers for comparison
A
Uniform outer vanes in black tailed birds
Pigment spread. S U
B
Light outer vanes in black tailed birds.
Pigment clumped. S u
C
Uniform outer vanes in blue tailed birds
Pigment clumped. s U or s u
D
Light outer vanes in blue tailed birds.
Pigment clumped. s U or s u

FIGURE 8.—Uniform and light outer vanes in *S* and *s* birds. Another tail feather is shown in each case for comparison.

correspond to the other tail feathers. The light condition (figure 8D) of the outer vanes of blue-tailed birds appears to be due to a diminution in the amount of pigment. The difference, then, between light and uniform outer vanes in *S* birds is due to clumped and spread pigment, while an apparently corresponding condition in *s* individuals depends upon the amount of pigment, which is clumped in both cases.

The foregoing may be explained on the assumption that a factor *U* spreads black pigment in the outer vanes of outer tail feathers of *S* birds, while *u* clumps it. Since *s* has already produced clumping in the tail region of blue-tailed birds the effect of *u* is not noticeable, and apparently *U* can not act in the presence of *s*. Still there is no reason to believe that *s* birds can not carry *U*.

FIGURE 9.—Uniform outer vanes in a blue-tailed bird. (Wisconsin No. 1704F.)

Before taking up the data in substantiation of such a theory two points must first be considered. The first is the variation in the degrees of lightness exhibited by different individuals. This is due in both black and blue-tailed birds to differences in the amount of pigment. It may depend, also, upon the age of the birds, younger ones showing more pigment than older ones. In fact it was found from a study of the several descriptions of many individuals that the first frequently gave the outer vanes as "uniform," while later descriptions, made after the birds had moulted, often gave them as "light." This was true of both types of birds. As a consequence the left outer tail feathers were plucked from squabs of various ages to determine whether this, like a normal moult, would tend to decrease the amount of pigment in the incoming feathers.

Such proved to be the case, as illustrated in figure 10, which represents 2 and 3 plucks from twelve birds. In view of the foregoing it was necessary to use only old birds, or squabs from which one of the outer tail feathers had been plucked at least once, before compiling the tables which follow.

The second point for consideration is lightening due to factors other than *u*. In certain cases of black-and-white-mottled birds the outer vanes may be light but such pigment as is present is spread, which probably indicates the action of factors for white spotting. Conse-

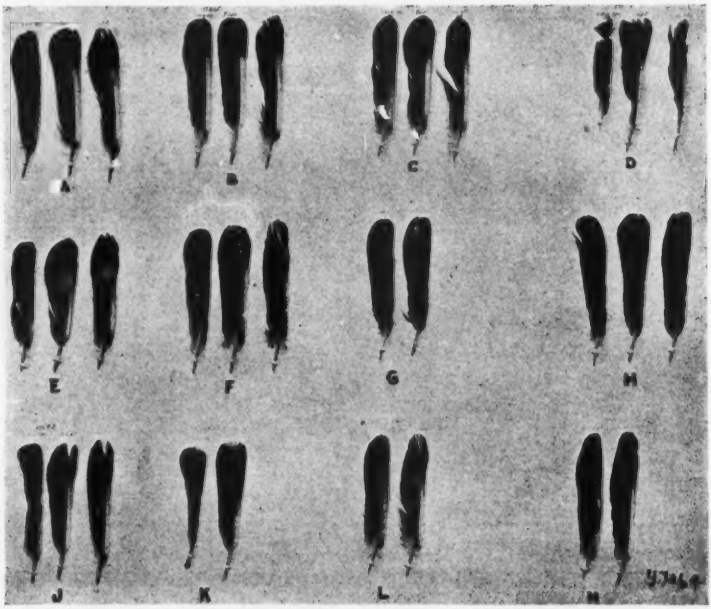

FIGURE 10.—Outer tail feathers of squabs, plucked successively upon their regrowth, showing the acquirement of light outer vanes in the later feathers.

quently in any doubtful cases a microscopic examination was necessary. The factors for white spotting are not included in the consideration of light and uniform outer vanes, but only *U* and *u*.

The dominance of *UU* in the presence of *SS* was indicated by seven matings which produced thirty-six uniform-outer-vaned offspring. The homozygous condition of *U* was judged from the offspring. No mating producing less than five individuals was used except in one case where

the pedigrees of the parents indicated their compositions. In the other matings some of the birds were "original" and consequently were unpedigreed, while others having pedigrees showed *b* or *s* or *A* birds in their immediate ancestry, making it impossible to judge of their composition.

Other matings showed the segregation of *Uu* in the presence of *SS*. Three matings in which both parents were *Uu* produced 18 "uniform" and 4 "light" black-tailed offspring, which is, considering the numbers, fairly close to expectation (16.5 : 5.5). Two matings of *Uu* to *uu*, from which a 1 : 1 ratio is expected, gave 10 : 11.

If *u* is a definite factor independent of *S*, then when *SSuu* or *Ssuu* birds are bred either *inter se* or to *s* individuals of the composition *uu*, all the *S* offspring should have light outer vanes. This condition has been only partially tested. An *Ssuu* (figure 8B) bird was bred to an *s* bird with light outer vanes (figure 8D), the condition of which with respect to *U* could not, of course, be phenotypically judged. From such a mating, however, nine offspring resulted, five *S* and four *s*, all of which had light outer vanes. Three of the *Ssuu* offspring were in turn mated to light-outer-vaned *s* birds and produced 26 offspring. Fourteen of these were blacks (*S*), and all, with the exception of one which died young before the first-plucked outer tail feathers had been replaced, had light outer vanes. This showed fairly conclusively that the original bird tested was of the composition *Ssuu*. Furthermore, the *s* bird to which it was mated, also evidently lacked *U*, as did the *s* birds to which the three *Ssuu* offspring of the original pair were bred.

When, however, two *Ssuu* (figure 8B) were bred together they produced an *SU* (figure 8A) individual, which is a decided exception and no explanation for which is at present apparent. This is a weak point in the theory, for only *u* birds should have resulted. It is recognized that the data which are presented in substantiation of the foregoing hypothesis are few, and in order to further strengthen it more *SSuu* and *Ssuu* birds should be thus tested. In this event another theory might better explain the data, but with the present records the present hypothesis seems to be the most satisfactory one available.

If, as supposed, *U* is unable to act in the presence of *s*, any definite breeding behavior of so-called light- and uniform-outer-vaned *s* birds is not expected. Of 51 matings of phenotypically light-outer-vaned blue-tailed birds bred *inter se*, four threw some offspring which had uniform outer vanes (figure 8C). As already mentioned, however, the point of difference is amount of pigment, so naturally the *U* factor just postulated would have no apparent effect. These four matings refer only to

those in which offspring were of a sufficient age to have passed through at least two or three moults or have had their outer tail feathers plucked several times. Seven other matings also show the production of uniform-outer-vaned offspring, but these individuals died young, and hence are not considered in this connection for reasons previously mentioned.

To show further that so-called uniformity in *s* birds is not the same as in *S* individuals, two so-called uniform-outer-vaned blue-tailed birds were bred to light ones and only light-outer-vaned offspring (16 in number) resulted. This plainly indicates that the genetic relation of the light and uniform conditions in *s* birds is complicated.

TABLE 6

Matings of SsUu birds × Ssuu birds.

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OBSERVED			EXPECTED		
							SU	*Su*	*sU+su*	*SU*	*Su*	*sU+su*
554+	450X	Dun	*Ssuu*	450Y	Dun	*SsUu*	5	1	1	2.54	2.54	1.76
662+	493B	Black	*Ssuu*	454B	Black	*SsUu*	4	7	1	4.04	4.04	2.76
1047+	829B	Dun	*SsUu*	829A	Dun	*Ssuu*	1	1	1	1.14	1.14	.76
1024+	901B	Black	*SsUu*	890B	Dun	*Ssuu*	(1*)	1	1	.75	.75	.50
Total (4 matings)							10	10	4	9	9	6

* Died young, therefore omitted from consideration.

Table 6 gives matings of *S* and *s* birds from which a 3:3:2 ratio is expected. The numbers are small (10:10:4) but approach the calculated (9:9:6) rather closely. Table 7 shows thirteen matings from which if the *s* birds are *Uu* a 3:1:4 ratio is expected and if they are *uu* a 1:1:2. They are known from pedigree and offspring to be of one or other of these compositions. The closeness of fit (P) for the first of these ratios is poor but for the second, good. There are, however, doubtless both *U* and *u* birds among those which are *s*. If it is assumed that half are *U* and half *u*, the expected ratio would be 5:3:8 (3:1:4+2:2:4). The closeness of fit on this assumption is excellent, χ^2 being less than 1. The numbers are, to be sure, small and consequently not too much importance is to be placed upon them, but the ratio at least lies between 3:1:4 and 1:1:2. It may, therefore, be assumed that the *s* parents comprised both *Uu* and *uu* individuals.

In order to prove further that *s* birds carry *U*, blue-tailed individuals with phenotypically light outer vanes have been bred to *Ssuu* individuals, n which case any *SU* offspring must have gotten *U* from its *s* parent.

TABLE 7

Matings of SsUu birds × ssUu or ssuu birds.

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OFFSPRING		
							SU	*Su*	*sU+su*
826+	6A	Black	*SsUu*	639B	Silver	*ss*{*Uu*, *uu*}	1	1	4
837+	639A	Silver	*ss*{*Uu*, *uu*}	719B	Black	*SsUu*	2	1	2
1448	1341D	Blue	*ss*{*Uu*, *uu*}	915B	Dun	*SsUu*	7	1	3
1454	1385B	Black	*SsUu*	1242A	Blue	*ss*{*Uu*, *uu*}	5	1	3
1472	829B	Dun	*SsUu*	1296N	Blue	*ss*{*Uu*, *uu*}	3	2	5
1605	1341D	Blue	*ss*{*Uu*, *uu*}	1500H	Dun	*SsUu*	1	1	4
1681	1512R	Black	*SsUu*	1657Z	Blue	*ss*{*Uu*, *uu*}	.....	1	3
1682	1448T	Black	*SsUu*	1668A	Blue	*ss*{*Uu*, *uu*}	.....	2	7
1693	$1593C_2$	Black	*SsUu*	$1607B_2$	Check	*ss*{*Uu*, *uu*}	.....	1	1
1695	1568B	Black	*SsUu*	1607U	Check	*ss*{*Uu*, *uu*}	1	1	1
1745	1638A	Blue	*ss*{*Uu*, *uu*}	1484A	Black	*SsUu*	.....	1	1
1761	1455V	Blue	*ss*{*Uu*, *uu*}	1553B	Black	*SsUu*	2	2	1
1773	1568B	Black	*SsUu*	1296N	Blue	*ss*{*Uu*, *uu*}	2	1	3
Total (13 matings)							24	16	38
Expected:									
1. If *s* birds are *Uu*, a 3:1:4 ratio is expected.....							28.89	9.63	38.52
2. If *s* birds are *uu* a 1:1:2 ratio is expected.....							19.50	19.50	39.00
3. If one-half of the *s* birds are *Uu* and the other half *uu*, a 5:3:8 ratio is expected.....							23.35	14.61	38.96

1. $\chi^2 = 5.0443$ P = .0806
2. $\chi^2 = 1.178$ P = .5620
3. $\chi^2 = .173$ .....

Of some twelve birds tested seven have been found to be *SU*, which upholds the above presumption. There are two matings on which data are lacking because in each an *S* squab died before the replacement of the first plucked feather.

Evidently there is a decided interaction of *S*, *U*, and their allelomorphs. *S* permits of the phenotypic expression of both *U* and *u*, while *U* can not express itself in the presence of *s*. Since both *u* and *s* produce the same effect, namely a bluing due to clumped pigment, they are indistinguishable

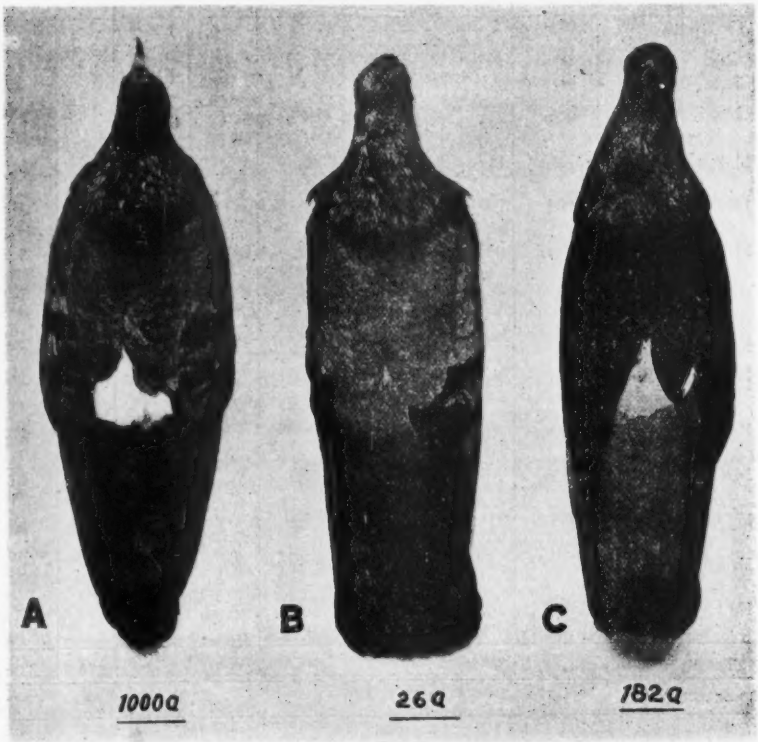

FIGURE 11.—A. Extreme light rump (grade 1) in blue black-barred wild Rock pigeon. (Wisconsin No. 1000A.) B. Uniform blue rump (grade 3) in blue black-barred common pigeon. (Wisconsin No. 26A.) C. Very slight check with light blue rump (grade 2). (Wisconsin No. 182A.)

when combined. No definite factor was found for the difference in amount of pigment in the outer vanes of *s* birds.

LIGHT AND UNIFORM RUMP

The two rump colors "white" and blue, found respectively in *C. livia*, particularly common in Europe, and *C. intermedia* of India, have long

attracted the attention of naturalists. This is the one mark of differentiation between these two species. According to SALVADORI (1893, p. 255), however, some specimens of *C. livia* may have the blue rump, in which cases they are indistinguishable from *C. intermedia*. In fact SALVADORI (p. 256) states that "every ornithologist knows the difficulty of drawing the exact line between *C. livia* and *C. intermedia*." This question is discussed in some detail by DARWIN (1868) and others already cited. The former attributes the difference in color of these two types to climate, the warmer environment of India tending to produce a color uniform with the rest of the bird.

"White" and blue rumps (figures 11A and 11B), together with many intermediate shades, also exist in barred and checked birds of several varieties of domestic pigeons. A detailed examination of many birds of the intense series admits of three fairly definite categories. Only intense individuals were used, as those of the dilute series presented another, but presumably strictly parallel, range of much lighter shades which were more difficult to classify.

The first or lightest grade is the "white" rump, typical of *C. livia*. This is preferably termed "extreme light blue" because a microscopic examination shows the presence of a small amount of clumped pigment, while white implies the absence of any pigment. The first grade is indicated below as number 1.

s Blue-tailed
1. Rump extreme light blue—typical of *C. livia* (figure 11A).
2. Rump light blue—several shades of light blue (figures 5 and 6).
3. Rump uniform blue—typical of *C. intermedia* (figure 11B).

S Black-tailed
4. Rump dark blue—found in some black birds (figure 12).
5. Rump black—uniform with the rest of the plumage (figure 1).

The next grade (number 2), found very frequently in general stocks of pigeons, is light blue. This color is not suggestive of white but of a silvery blue. Furthermore, the range of shades in this class is rather wide, extending from a very light blue, distinct from grade 1, to a shade just perceptibly lighter than uniform blue, grade 3. Uniform blue, as suggested in the first paragraph, refers to the correspondence in shade between rump, back and wing coverts. The pigment is clumped in grades 1, 2 and 3. The amount of pigment is apparently the determiner of the

various shades, the lighter ones having less pigment than the darker. There are, then, at least three color-grades of rump in the *s* or blue-tailed birds, depending upon the amount of clumped pigment.

A consideration of rump conditions in black-tailed birds reveals two fairly definite types. Certain *S* individuals may be solid black except for a lighter shade of rump, the feathers of which give a dark blue appearance, (grade 4). It is a darker blue than any above described. The pigment, however, is clumped as it was in each of the foregoing cases. This grade, like the light blue (2), shows some range in shade, but for present purposes these shades will all be considered together under 4.

The last type (grade 5) occurs in *S* individuals and refers to a black rump uniform with the rest of the black plumage. In this case the pigment is spread.

These conditions are analogous to those found in the outer vanes of outer tail feathers of both blue- and black-tailed birds. In both cases the pigment is clumped in *s* birds and the shade depends upon the amount of pigment present. The dark blue rump of black birds corresponds to the light condition in the outer vanes of *S* birds in that the pigment is clumped, while the black rump and uniform outer vanes both have spread pigment.

The genetic analysis of the rump conditions is, however, more difficult than that of the outer vanes. The work of STAPLES-BROWNE (1908, 1912) is, so far as the writer is aware, the only report on the definite inheritance of these characters. His records are based on breeding tests of *s* birds only. Extreme-light-blue rump (1) appears to be dominant to uniform-blue (3), to segregate fairly cleanly, except for the appearance of some light blues (2), and uniform blue breeds true. He classes the light blues (2) with the uniform blues (3). WHITMAN (1919, vol. 2, table 87c, p. 112) obtained a uniform-rumped individual from a pair of presumably extreme-light-blue-rumped (1) wild *C. livia*.

The writer has collected considerable data from many matings and in certain cases obtained results corresponding to those of STAPLES-BROWNE. When, for instance, extreme-light-blue-rumped (1) birds were bred to light-(2) or uniform-blue-rumped (3) ones, all three types resulted. From fourteen matings of uniform-blue rumps (3), bred *inter se*, types 2 and 3 resulted, while one such mating also produced grade 1. This latter case is not in keeping with STAPLES-BROWNE'S findings. The writer's data correspond to those of STAPLES-BROWNE in that types 1 and 3 do not segregate cleanly when crossed, but produce light blue rumps (2). As previously stated STAPLES-BROWNE considered these latter as uniform blues (3). It has been found, however, that the light shades, when bred

together or to uniforms, throw extreme-light-blue-rumped (1) offspring as well as uniform (3)- and light-blue (2)-rumped individuals.

In view of these discrepancies the writer made another classification for all matings,[8] including types 1 and 2 under one head and type 3 under the other, whereas STAPLES-BROWNE made one class of type 1 and combined 2 and 3. On such a basis as the former, that is, making a single class of 1 and 2, and one of 3, results are equally confusing. When extreme (1) or light (2) blues heterozygous for (3) are bred together, all three types result in a proportion of 3 : 1 (37 : 13), types 1 and 2 being combined to form the larger class. If heterozygotes, grades 1 and 2, carrying 3, as indicated by pedigree, are crossed on grade 3, the assumed recessive, the results of thirteen matings show 30 : 54 in the respective classes, that is, twice as many recessives as dominants. Type 3 does not breed true, but produces as many extreme and light blues (1 and 2) as uniform (3), the numbers being 37 : 39 from 14 matings. Obviously, then, this scheme comes no nearer to explaining the inheritance of rump conditions in *s* birds than did that of STAPLES-BROWNE.

Further instabilities are encountered when the breeding behavior of the dark blue (4) rump of black birds is considered. As already mentioned STAPLES-BROWNE'S data related to *s* birds only. Dark-blue-rumped (4) *S* offspring may be obtained from light(2)- or extreme-light(1)-blue-rumped birds, crossed on black-rumped (5) blacks. When these dark blues (4) are mated together they may produce a very small proportion of individuals like themselves (1 in 21 offspring), and they may throw some light (2) *s* offspring. Three matings of type 4 by type 2 produced all five types. Similarly, when grade 5 is crossed on grade 3 (24 matings) the five types result. If, on the other hand, black rumps (5) are mated to black rumps (17 matings) an occasional grade 2 may appear, but the majority belong to grade 5.

Evidently the inheritance of the various rump conditions in blue- and black-tailed birds is due to a complicated interaction of factors. In order to obtain the correct genetic analysis more detailed breeding experiments must be undertaken.

THE RELATION OF THE DULL-BLACK CHECK TO DEEP AND DULL BLACK

The modifications of black dealt with so far have been due to the relative amounts of the so-called colors, blue and black, exhibited by certain

[8] Only those birds for which rump feathers have been saved or the descriptions record "Rump lighter than wing coverts," or "Rump same shade as wing coverts," have been used in these tables.

individuals, or in other words to the encroachment of clumped pigment upon spread. There is another diversity of black of another sort in that it does not involve bluing but is a modification of the depth and sheen of the color of many black birds. Some individuals may have either a brownish or a powdery plumbeous cast instead of a deep uniform velvety one. These conditions are considered undesirable by breeders of black varieties of pigeons. CHAPMAN (1911) calls attention to them as "very grave defects."

Furthermore, some of these birds may show darker indistinct wing bars in the usual position (figure 13) or in some cases check marks lighter than the general color in the wing coverts (figure 12). These are due to two shades of black instead of the usual blue and black of the epistatic series described in earlier sections of this paper. BOITARD and CORBIÉ (1824)

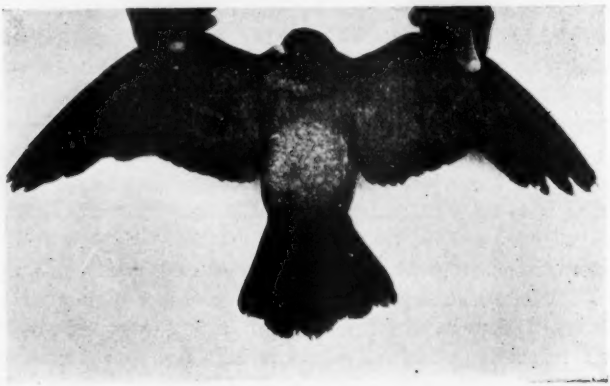

FIGURE 12.—Dull black check with dark blue rump (grade 4) and light outer vanes of outer tail feathers. (Wisconsin No. 1827C.)

mention the cropping out of indistinct wing bars on black birds in certain crosses.

Checks and bars of this description are likewise prevalent among duns (dilute blacks). The two main differentiating points between checks of this type, that is, dull-black or dun, and the blue type, are, first, the absence of the typical blue or silver tail with a black or dun terminal band, and second, the production of checks and bars by two shades of black or dun, and not by black and blue or dun and silver. In other words these checks and bars carry *S* while the blue type does not. These two points are further emphasized when the pigment-granule arrangement is studied, for all pigment in the dull-black or dun checked birds is

in a spread condition. It is, however, more dense in the wing bars and darker areas surrounding the check marks than in the checks themselves and regions about the wing bars. The deeper-colored areas correspond to the black of barred and checked birds of the blue-black epistatic series, while the lighter areas correspond to the blue color.

Unfortunately breeding data on these patterns are very few. There are, however, several matings which give the breeding behavior of dull black (*d*) without bars or checks as contrasted to deep black (*D*). The chief distinguishing characteristics between this factor and *I* which affects density are (1) *D* is not like *I* in being sex-linked, (2) the difference in shade between *d* and *i* birds is readily distinguishable and (3) so far as is known at present, *d* individuals are indistinguishable from *D* in the presence of *i*.

FIGURE 13.—Dull black with blacker bars, uniform rump (grade 5) and light outer vanes of outer tail feathers. The light appearance of the rump is not due to bluing but to a very dull black. (Wisconsin No. 1761J.)

The data on the relation of *d* and *D* in blacks are presented, because, to anticipate a little, it seems evident that the *d* condition is necessary for the manifestation of the two patterns. *D* does not permit of the presence of any contrasting shade or color, for birds carrying it are deep blacks uniformly pigmented.

This character, like that of the outer vanes of the outer tail feathers, changes with age. Most if not all black squabs are dull, and not until they have moulted at least once does the deep plumage, if they are to have that as adults, appear. Accordingly only adults are considered in the following discussion.

Certain black Baldheads and self-black Tumblers that have been used in this work have had the desirable deep-black feathering. Two matings of such black Baldheads produced four offspring deep-black like their parents, indicating that one or both of the parents were homozygous for *D*. Three matings of "original" deep-black Tumblers bred to deep-black checks gave a different result. "Checks" in this connection refers to the blue or *sC* check, in which the black can be either dull or deep. Since the Tumblers were original birds their genotypic compositions were unknown. The checked parents were, however, from colony stock and known to be *Dd*. As both deep and dull blacks were produced it was concluded that the Tumblers were likewise heterozygous. There were 12 of the former and 8 of the latter, where a 3:1 ratio was expected.

As just mentioned, the checks employed here refer to the *sC* of the epistatic series. Since such individuals present both blue and black, obviously the shade of black can be determined providing the black area of the wings is large enough, that is, if it occupies as much space on the wings as does the blue. A fairly large black region is necessary in order to admit of comparison. This was further emphasized when an attempt was made to compile data on the shade of black from bars and extreme checks. This was found impossible. As a consequence only blacks, black blue-rumps and slight to medium checks are used in these tables.

Table 8A shows six matings of heterozygous deep blacks bred to dull blacks, giving 14 deep to 11 dull blacks where the expected is 12.5:12.5. Section B shows the same thing except that some of the parents are *sC* checks. In this case the results are 14:16 and the expected is 15:15. A total for the 14 matings gives 28 to 27 where equality is anticipated.

Thirteen matings of dull to dull demonstrated the true-breeding behavior of this character, forty-four dull and no deep offspring being obtained. Obviously, then, the difference between dull and deep black is a single factor.

As previously mentioned, it is fairly apparent that *D* birds can not display the dull-black check and bars, because this would necessitate the introduction of poor black in deep-black individuals, which very evidently is not in keeping with the deep-black character. If this is the situation the present type of check, like the blue of the epistatic series, is due to an interaction of factors. That is, *d* is necessary for its manifestation as *s* is for that of the blue check, but the former carries *S* while the blue type lacks *S*. In the former respect the *s* and *d* conditions are analogous. The two checks may be termed the *sC*, typical of *C. livia*, and the *dS*, that just described.

TABLE 8

*Deep black (Dd) by dull black (dd).**

MATING	♂♂	COLOR	COMPOSITION	♀♀	COLOR	COMPOSITION	OFFSPRING	
							D	*d*
A. Blacks by blacks								
120+	45B	Deep black	*Dd*	56A	Dull black	*dd*	4	1
575+	448A	Deep black	*Dd*	432B	Dull black	*dd*	1	1
835+	719A	Dull black	*dd*	727A	Deep black	*Dd*	3	7
1317	1015B	Deep black	*Dd*	1127B	Dull black	*dd*	2	
1812	1685C	Deep black	*Dd*	$1594Q_3$	Dull black	*dd*	4	
1826	$1574F_2$	Deep black	*Dd*	1594R	Dull black	*dd*		2
Total (6 matings)							14	11
Expected							*12.5*	*12.5*
B. Black by check and check by check								
168+	28B	Dull black	*dd*	71A	Deep black check	*Dd*	4	5
1153+	972A	Deep black check	*Dd*	559A	Dull black check	*dd*	1	1
1346	972A	Deep black check	*Dd*	1033H	Dull black	*dd*		1
1684	1665A	Deep black check	*Dd*	1677A	Dull black	*dd*		1
1692	$1553J_2$	Dull black	*dd*	1616X	Deep black check	*Dd*	4	3
1693	$1593C_2$	Deep black	*Dd*	$1607B_2$	Dull black check	*dd*	1	
1695	1568B	Deep black	*Dd*	1607U	Dull black check	*dd*	1	1
1699	1657K	Deep black check	*Dd*	1605V	Dull black	*dd*	3	4
Total (8 matings)							14	16
Expected							*15*	*15*
Total for 14 matings							28	27
Expected							*27.5*	*27.5*

* Only adult birds considered.

CHECK MARKINGS IN THE COLUMBIDAE

The preceding evidence leads to the conclusion that the domestic pigeon presents two types of checks and bars, due to the interaction of at least three different factors, and varying in pigment-granule arrangement and density of pigmentation. It was pointed out in the introduction that there

were several species closely related to *C. livia* which resembled the barred form and one or two the checked. These also correspond to the same patterns in the domesticated pigeon. The dull-black check described in the preceding section for domesticated varieties is a regular marking in *C. guinea*, closely related to *C. livia*. The check marks, which are V-shaped and situated at the tips of the wing coverts, are lighter than the surrounding areas, but the pigment is, in general, spread in all parts of the feathers. There is, however, a tendency to clump near the tips of the barbules, especially in the region of the V-shaped check mark.

These two types are found only in those forms closely related to *C. livia*. But there is another check condition which obtains in certain species outside the Columba group. In these the check marks instead of being lighter than the surrounding areas, as is usual in both the blue and dull-black checks, are darker than the rest of the plumage. Examples of this type are to be found in the mourning dove (*Zenaidura macroura carolinensis*) and the European turtle dove (*Turtur turtur*). In the former the few checks are located in the region of the usual wing bars of *C. livia*, and are black against the surrounding brown plumage. The dark checks of the turtle dove occupy the entire centers of the wing coverts, which are edged with a lighter shade.

Sufficient breeding data relating to the inheritance of this type of check are lacking. Microscopic examinations have been made, however, of the feathers of several individuals representing various species chosen at random. In all cases the pigment was spread throughout the feathers but was more dense in the dark check marks than in the lighter surrounding areas. This is just the reverse of the dull-black check, in which case the check is lighter than the rest of the feather, being the area of lesser pigmentation. It will be noted that in both cases all the pigment is spread, the differentiation of the pattern being based on density of pigment and not on arrangement of granules. The forms in which this condition was studied were *Zenaidura macroura carolinensis*, *Turtur turtur*, *Turtur lugens*, *Columbigallina rufipennis*, *Geopelia striata* and *Oena capensis*.

GENERAL DISCUSSION

The work by COLE (1914) and the present work on blue and black color in pigeons deal with two types of interacting factors. Both are dependent upon B^9 for their phenotypic expressions. All the factors of the first group, belonging to the epistatic series, produce similar effects, namely, clumping and spreading pigment. Each, however, is limited in its action

[9] See footnote 6, p. 486.

to a particular region. For example, the factor for barring, B_a, spreads pigment in the wing-bar region, that for sooty, S_o, introduces a sprinkling of black color in the wing coverts, which may acquire definite black spots resulting in a checked appearance when C, the checking factor, is added. In this case the sooty areas become distinctly black by the addition of more spread pigment. Similarly, the effect of the checking factor is concealed by the full spreading of black to the wing coverts leaving either a blue rump and tail or only a blue tail, when T is present. T in turn is hidden by S, which spreads pigment throughout the plumage of the individual, making it a solid black. The epistatic series, then, consists of a set of factors each of which increases the area of spread pigment over that of its predecessor. Or, in other words, the respective dropping out of each of the several factors is necessary for the phenotypic expression of those lower in the series.

The factors of the second group, namely, those for uniform and light outer vanes of outer tail feathers, uniform and light rump, and deep and dull black, are dependent upon B and S for their various expressions. They do not, however, lie in the epistatic series but interact differently. U, for uniform outer vanes of outer tail feathers, can express itself only in the presence of S, being indistinguishable in all s birds.

The several rump conditions vary somewhat similarly in black- and blue-tailed birds. Dark blue rumps are known to exist in S birds. They might, however, be found in the extreme type of black blue-tails (sT) in which ordinarily the tail is blue and the rump black like the wing coverts. This is pure supposition, as no birds of this description have been identified. Below these the rump colors change to those described for s birds.

Both I and the higher stages of the epistatic series, S, T, and some grades of C, are necessary for deep and dull black to make themselves apparent.

There are, then, two types of interacting factors, those of the epistatic series behaving in an orderly serial fashion, and others which are dependent upon certain stages of the series for their various expressions.

With the isolation of the several factors of the epistatic series comes the fact that the previously postulated ratios between S and s birds are changed. For example, it was pointed out above (p. 480) that COLE (1914) considered all checks (only checks were involved in the three illustrative matings used by him, no black blue-tails or sooties) as blacks and consequently he expected three blacks and checks to one barred. Since, however, the existence of the checking factor has been determined, the former 3:1 ratio becomes a 15:1, as two factors instead of one are involved. If, on

the other hand, the present interpretation is correct, blacks heterozygous for *S* when bred *inter se* should give a 3:1 ratio, considering black blue-tailed birds and all individuals below them in the series as *s*. The combined available data fit this ratio well, with the observed numbers 71:28 and the expected 74.25 : 24.75. The probable error (P.E.) of the ratio is .12 and the $\frac{\text{Dev.}}{\text{P.E.}}$ is 1.08. Similarly, in the data giving an expected 1:1 ratio the total observed were 43:55 and the expected 49:49. The P.E. in this case is .068 and the $\frac{\text{Dev.}}{\text{P.E.}}$ is 1.47. These results are in keeping with the present hypothesis.

Unless some stage shall be found that is dependent upon *S*, the ratio between *S* and *s* will continue to remain the same. If, however, more intermediates involving both *S* and *s* should later be isolated, the various ratios existing between the present known factors will become altered. It seems, furthermore, highly probable that more factors are concerned, since the series appears to grade from black through to a pure blue wing lacking any black except that confined to the tips of the primaries, secondaries and tertiaries. If six grades in this series have been shown to exist independently, there is no reason why others could not also be split off, for students of Drosophila have found seven modifiers acting on one eye color alone, eosin, which in its turn lies in the graded multiple-allelomorph series from red to white.

As the members of the epistatic series increase, the chances for the occurrence of the recessives, especially those lower in the series, as the barred type, decrease. In fact, with the series as it now is, sooties and bars should appear rather infrequently if all the intermediate factors were involved. This, however, is not the case, but in several instances the number of barred birds, especially, is high. This is due, no doubt, to the fact that most of the birds making up the parents of the various matings are not heterozygous for all the characters under consideration, but for only one or two. In such a case more recessives of these types, are expected.

That the check series seems to grade almost imperceptibly from one type to another and is epistatic, is quite in keeping with WHITMAN'S selection experiments. He was able to select for less check but not for more. These results led him to believe that the evolution of checks and bars was an indistinguishable and gradual one moving in one direction. It does not, however, necessarily follow that because the interaction of these several factors produces an apparent epistatic series, the mutations producing the various grades of spread pigment occurred in any particular

order. This is made even more unlikely by the fact that these factors are apparently independent and hence exist at different places in the germplasm.

The isolation of some of these factors, as particularly that for check, and a study of the various rump conditions are of interest not only from the evolutionary standpoint but also from the systematic. Certain characters governed by these factors have been used as marks of distinction between species. As pointed out earlier, SALVADORI admits that rump color is the only tangible difference between *C. livia* and *C. intermedia*. In the case of checks and bars in the wild Rock, DARWIN suggested that these two forms should be considered as a single species. He even went further and stated that several other species as *C. rupestris*, *C. schimperi* and *C. gymnocyclus* should also be included with *C. livia*. In view of the present knowledge of Mendelism, DARWIN'S suggestions are even more valid, since in certain of these cases at least, it seems evident that the species differences are based on a single factor. WHITMAN'S classification of *C. affinis*, which is checked, and *C. livia*, which is barred, illustrates this point.

Here the difference is presumably due to a single factor, *C*. If such marks are used for species differentiation, then the color variations of each variety of the various breeds of pigeons might as legitimately be assigned species names.

It seems possible, therefore, in view of the foregoing and the close resemblance in descriptions given by SALVADORI, of the species closely related to *C. livia*, that the domesticated pigeon may be, as suggested by GHIGI (1908), of polyphyletic origin and not descended from a single species, *C. livia*.

SUMMARY

1. The present paper is a study of several interacting factors which produce varying amounts of black and blue color in pigeons.

2. The basic factor concerned is *B*, producing black pigment.

3. The first group of factors consists of five which belong to the epistatic series. The lowest is B_e, spreading black pigment in the wing bars; the next is S_e, which produces a sprinkling of black in the wing coverts; the third is the checking factor, *C*, producing the well known check pattern; the fourth, *T*, spreads black throughout the wing coverts, leaving a blue tail,—this is the black blue-tail pattern; *S* is the highest member of the series, spreading black pigment throughout the tail, thus producing a full-black.

4. The inheritance of *C* has been amply proven, while that of the other factors is only indicated. All, however, have been shown to lie in an epistatic and not in a multiple-allelomorph series.

5. A factor *U* and its allelomorph determine uniform and light outer vanes in *S* birds, being indistinguishable in the presence of *s*.

6. Five rump conditions studied in black- and blue-tailed birds have been found to be due to a complicated interaction of factors independent of the epistatic series.

7. The density of black pigment is due to a single Mendelizing factor, *D*. This differs from *I* in that it is not sex-linked, and the shades of black resulting from it are not as light as the darkest duns.

8. A check and barred pattern due to two shades of black or dun and not to black and blue or dun and silver have been found to occur when *d* is present. The inheritance of these patterns has not been worked out.

9. The orderly fashion of behavior of the members of the epistatic series led WHITMAN to believe that checks and bars developed orthogenetically.

10. The orderly behavior of these factors is no criterion that the mutations producing them occurred in the same order.

11. If closely related species are found to differ from each other mainly by heritable color factors, they might on such a basis be included in a single species.

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SELECTION THROUGH THE CHOICE OF SEEDS FROM DOMINANT PLANTS OF AN ALLOGAMOUS POPULATION[1]

RAINARD B. ROBBINS

University of Michigan, Ann Arbor, Michigan

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INTRODUCTION

Consider the problem of selection involved in choosing seeds from plants showing a certain dominant character, while no effort is made to influence the source of pollen. In the following discussion the fate of a single Mendelian character will be studied under such mating.

The conclusion can be stated thus: *The limiting population resulting from the type of mating in question is all of one class, pure dominants.* It is interesting to contrast this conclusion with the fact, repeatedly pointed out in recent years, that in unrestricted random mating the proportions of pure dominants, heterozygotes and recessives are fixed after a single operation of random mating.

DISCUSSION

Let

(1) $\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots r_{n-1}AA+s_{n-1}Aa+t_{n-1}aa$

represent the $(n-1)$th generation resulting from the type of mating in question, the coefficients being so chosen that

(2) $\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots r_{n-1}+s_{n-1}+t_{n-1}=1$

The gametes producing the next generation will be in the following proportions:

$$\text{Males:} \quad \frac{(2r_{n-1}+s_{n-1})}{2}A+\frac{(2t_{n-1}+s_{n-1})a}{2}$$

$$\text{Females:} \quad \frac{(2r_{n-1}+s_{n-1})}{2\,K_{n-1}}A+\frac{s_{n-1}a}{2\,K_{n-1}}$$

[1] This problem was suggested to the author by Mr. L. E. THATCHER, Assistant Agronomist, OHIO AGRICULTURAL EXPERIMENT STATION, Wooster, Ohio. This STATION, under the direction of the Agronomist C. G. WILLIAMS (present Director of the STATION) has carried out the type of selection in question during a period of fifteen years, in experiments with corn. A report of progress was published in 1915 in Ohio Experiment Station Bulletin 282; "Corn experiments." A complete report is now being prepared.

where $K_{n-1}=r_{n-1}+s_{n-1}$. For convenience we will use for the above proportions,

Males: $M_{n-1}\,A+N_{n-1}a$
Females: $U_{n-1}\,A+V_{n-1}a$

It is evident that the composition of the generation formed by the union of the above gametes is

$$M_{n-1}\,U_{n-1}\,AA+(M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1})Aa+N_{n-1}\,V_{n-1}aa$$

The gametes produced by the individuals of this generation, which will enter the mating in question, are in the proportions indicated as follows:

Males:

$$M_n=\frac{2M_{n-1}\,U_{n-1}+M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1}}{2}$$

$$N_n=\frac{2N_{n-1}\,V_{n-1}+M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1}}{2}$$

Females:

$$U_n=\frac{2M_{n-1}\,U_{n-1}+M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1}}{2\,K_n}$$

$$V_n=\frac{M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1}}{2\,K_n}$$

in which

$$(3)\ldots\ldots\ldots\ldots\ldots\ldots\ldots K_n=r_n+s^n$$

Replacing

V_{n-1} by $1-U_{n-1}$ and
N_{n-1} by $1-M_{n-1}$

The above relations simplify:

$$M_n=\frac{2M_{n-1}\,U_{n-1}+M_{n-1}\,(1-U_{n-1})+U_{n-1}\,(1-M_{n-1})}{2}$$

$$=\frac{M_{n-1}+U_{n-1}}{2}$$

$$U_n=\frac{2M_{n-1}\,U_{n-1}+M_{n-1}\,(1-U_{n-1})+U_{n-1}\,(1-M_{n-1})}{2K_n}$$

$$=\frac{M_{n-1}+U_{n-1}}{2\,K_n}$$

$$K_n=r_n+s_n$$
$$=M_{n-1}\,U_{n-1}+M_{n-1}\,V_{n-1}+U_{n-1}\,N_{n-1}$$
$$=M_{n-1}\,(U_{n-1}+V_{n-1})+U_{n-1}\,(1-M_{n-1})$$
$$=M_{n-1}+U_{n-1}-M_{n-1}\,U_{n-1}$$

We thus have the following equations:

$$(4)\ldots\ldots\ldots\ldots\ldots\ldots\ldots M_n=\frac{M_{n-1}+U_{n-1}}{2}$$

$$(5)\quad U_n=\frac{M_{n-1}+U_{n-1}}{2\ K_n}$$

$$(6)\quad N_n=1-M_n$$

$$(7)\quad V_n=1-U_n$$

$$(8)\quad K_n=M_{n-1}+U_{n-1}-M_{n-1}U_{n-1}$$

From equation (4) and (5) we deduce,

$$(9)\quad K_n=\frac{M_n}{U_n}$$

It would be desirable at this point to solve the above equations, obtaining the solutions in terms of initial values and the variable n. This has not been accomplished.

Although the fundamental equations have not been solved explicitly, it can be proved, as shown below, that if this type of mating is continued indefinitely the population approaches more and more nearly pure dominant in character.

From equations (4) and (5) we have,

$$(10)\quad L_n=\frac{L_{n-1}}{2}\left[1+\frac{1}{K_n}\right],$$

where $L_n=M_n+U_n$. Similarly,

$$L_{n-1}=\frac{L_{n-2}}{2}\left[1+\frac{1}{K_{n-1}}\right],$$

and so on for decreasing values of n. Hence,

$$(11)\quad L_n=\left[1+\frac{1}{K_n}\right]\left[1+\frac{1}{K_{n-1}}\right]\left[1+\frac{1}{K_{n-2}}\right]\cdots\cdots\left[1+\frac{1}{K_2}\right]\frac{1}{2^{n-1}}$$

From equation (3), $K_n=r_n+s_n$, it is evident that $K_n<1$ for all values of n since from equation (2),
$r_n+s_n+t_n=1$ and t_n is always positive. Hence,

$$1+\frac{1}{K_n}>2$$

for all values of n. Therefore, referring to equation (10) we see that

$$L_n>L_{n-1}$$

for all values of n. But L_n can never be larger than 2, since

$$L_n=M_n+U_n \text{ and } M_n<1 \text{ and } U_n<1$$

It therefore follows that as n increases indefinitely L_n approaches a limit. Hence K_n approaches a limit and

$$\lim_{n=\infty} K_n = 1$$

for otherwise L_n would increase without limit (see equation (11)).
But $K_n = r_n + s_n$ and $r_n + s_n + t_n = 1$.

Hence

$$\lim_{n=\infty} t_n = 0$$

Going back to the method of mating, we note that

$$t_n = V_{n-1} N_{n-1}$$

Hence

$$(12) \quad \lim_{n=\infty} V_{n-1} N_{n-1} = 0$$

From equations (4), (5), (6) and (7) it is easy to deduce,

$$(13) \quad V_n = \frac{N_n - N_{n-1} V_{n-1}}{1 - N_{n-1} V_{n-1}}$$

From equations (12) and (13) it is evident that V_n and N_n approach limits as n increases indefinitely and that these limits are equal; i.e.,

$$(14) \quad \lim_{n=\infty} V_n = \lim_{n=\infty} N_n = 0$$

Thus the recessive gamete tends to disappear. Hence both the pure recessive and the heterozygous types tend to disappear as the mating in question is continued indefinitely.

In order to show how rapidly the limiting situation is approached the proportions have been calculated for a particular case. It is assumed that the original cross is between AA and aa, giving a population of the single type Aa. Random mating occurs in this population since no recessives are present to be excluded. The result is the F_2 population indicated by

$$\tfrac{1}{4}AA + \tfrac{1}{2}Aa + \tfrac{1}{4}aa$$

From this point on, selection occurs, since no aa plants are chosen as the source of seeds.

The following table gives the theoretical proportions of the three types of individuals in each generation resulting from the selection in question.

n	r_n	s_n	t_n
1	.0000	1.0000	.0000
2	.2500	.5000	.2500
3	.3333	.5000	.1667
4	.4083	.4667	.1250
5	.4706	.4339	.0956
6	.5226	.4025	.0750
7	.5664	.3736	.0601
8	.6035	.3475	.0491
9	.6352	.3241	.0407
10	.6626	.3032	.0342
11	.6864	.2845	.0292
12	.7072	.2677	.0251
13	.7256	.2526	.0218
14	.7419	.2390	.0191
15	.7565	.2267	.0169
16	.7695	.2155	.0150
17	.7813	.2053	.0134
18	.7920	.1960	.0121
19	.8017	.1874	.0109
20	.8106	.1795	.0099
21	.8187	.1722	.0090
22	.8262	.1655	.0083

Examination of the above table shows that of the twenty-second generation about 83 percent is of the dominant type, less than one percent is of the recessive type and the remainder, over 16 percent, is heterozygous. Furthermore, it will be observed that the proportions are changing very slowly. The indications are that probably twenty more generations would be necessary to raise the proportion of pure dominants to 90 percent of the whole population.

SUMMARY

In selection which consists in the choice of seeds from dominant plants, the composition of the resulting generations will approach more and more nearly pure dominant in character regardless of the composition of the original population if it is not all pure dominant in character.

It is to be noted, however, that the approach to the limiting population decreases in rapidity in succeeding generations.